40094

National Library of Canada | Bibliothèque nationale du Canada

CANADIAN THESES ON MICROFICHE | THÈSES CANADIENNES SUR MICROFICHE

NAME OF AUTHOR/*NOM DE L'AUTEUR* Art Borkent

TITLE OF THESIS/*TITRE DE LA THÈSE* Systematics and Bionomics of the Species of the subgenus Schadonophasma Dyar and Shannon (Chaoborus, Chaoboridae, Diptera)

UNIVERSITY/*UNIVERSITÉ* University of Alberta

DEGREE FOR WHICH THESIS WAS PRESENTED/*GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* M. Sc.

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1978

NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* Dr. G.E. Ball

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

DATED/*DATÉ* May 15, 1978 SIGNED/*SIGNÉ* A. Borkent

PERMANENT ADDRESS/*RÉSIDENCE FIXÉ* Dept. of Entomology,
University of Alberta.
Edmonton, Alberta T6G 2E3

NL-91 (3-74)

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

THE UNIVERSITY OF ALBERTA

SYSTEMATICS AND BIONOMICS OF THE SPECIES OF THE SUBGENUS SCHADONOPHASMA DYAR AND SHANNON (CHAOBORUS, CHAOBORIDAE, DIPTERA)

by

© ART BORKENT

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1978

Frontispiece: Chaoborus trivittatus adult male.

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SYSTEMATICS AND BIONOMICS OF THE SPECIES OF THE SUBGENUS SCHADONOPHASMA DYAR AND SHANNON (CHAOBORUS, CHAOBORIDAE, DIPTERA), submitted by Art Borkent in partial fulfilment of the requirements for the degree of Master of Science.

.....
Supervisor

.....

.....

Date April 25, 1978

Dedication

To my wife Annette, for sharing the pleasures and trials of this work, and more.

For thou didst create all things,
and by thy will they existed and
were created.

Revelation 4:11b

ABSTRACT

Study of structure, intraspecific variation, life cycles and bionomic features suggests the presence of three species of the subgenus Schadonophasma. Chaoborus trivittatus (Loew) and Chaoborus cooki Saether are restricted to North America while Chaoborus nyblaei (Zetterstedt) is known only from Fennoscandia. Chaoborus brunskilli Saether and Chaoborus knabi (Dyar) are conspecific with C. trivittatus.

All stages of each species were studied except first, second and third larval instars of C. nyblaei which are unknown. Eggs of C. cooki and C. nyblaei, unlike those of C. trivittatus, exhibit a thickened exochorion. C. cooki eggs are laid in a spherical mass with little gelatinous matrix while those of C. trivittatus are laid in a spiral arrangement in a disc of gelatinous matrix. First instar larvae of C. cooki possess a more pronounced egg burster than do those of C. trivittatus. All other stages can be distinguished only by using a combination of characters. A compound character index is provided for separation of fourth instar larvae of C. trivittatus and C. cooki and was used to test possibilities of conspecificity of these two species. Male adults can be identified by the shape of the penis valves and a ratio of the length of two wing veins.

The thickened exochorion of eggs of C. cooki and probably C. nyblaei, is an adaptation to overwintering as eggs in temporary ponds. C. cooki is univoltine. C. trivittatus immatures occur mostly in permanent ponds where this species overwinters as a fourth instar larva. This species may be uni- or multivoltine or have a two year life cycle.

Behavioral differences are evident between C. trivittatus

and C. cooki. Only C. cooki larvae are capable of ingesting ostracods. Male adults of C. trivittatus form large swarms. Adult females are the main dispersing agent of C. trivittatus while limited evidence for C. cooki suggests that both sexes of this species disperse. Under laboratory conditions C. trivittatus male adults live up to seven to eight days and female adults up to twelve days.

The pattern of intraspecific variation indicates that some of the variation of fourth instar larvae is due to sex-associated, age-related, and geographic variation. Geographical variation of characters of fourth instar larvae of C. trivittatus indicates that this species was present in Beringian refugium and that refugium south of the continental ice sheet during the Wisconsonian glaciation.

A reconstructed phylogeny of some Chaoborus species is provided. The subgenera Schadonophasma and Chaoborus s. str. are both monophyletic and are sister groups. An upper Oligocene Chaoborus fossil indicates the minimum age of the speciation events which gave rise to the ancestors of these two groups to be 25 million years.

A reconstructed phylogeny of Schadonophasma species indicates that C. cooki and C. nyblaei are more closely related to each other than either is to C. trivittatus. Zoogeographic considerations suggest two possible hypotheses for the origin of these species. The first invokes allopatric speciation between the Nearctic and Palaearctic regions producing C. trivittatus and the ancestor of C. cooki and C. nyblaei. Subsequent geographical isolation of populations of the latter lineage produced C. cooki and C. nyblaei. The second hypotheses differs in proposing that the C. cooki-nyblaei lineage arose in sympatry with C. trivittatus from individuals of a C. trivittatus-like ancestor that involved an overwintering egg stage which allowed

exploitation of temporary habitats. A model for the development of reproductive isolation in sympatry suggests the occurrence of a mutation resulting in a diapausing egg in the ancestral population. Through temporal disjunction of mating periods, homogamic mating, complete selection against overwintering larvae in temporary ponds and overwintering eggs in permanent ponds, the two lineages which gave rise to C. trivittatus and the ancestor of C. cooki-nyblaei became genetically isolated.

ACKNOWLEDGEMENTS

Many individuals have contributed to this study and I extend my thanks to them all. In particular, I express my sincere appreciation to my supervisor G.E. Ball, not only for cultivating my interests in entomology and particularly in systematics since our first encounter when I was yet in high school, but also for his cheerful enthusiasm and thoughtful direction throughout the course of this study. He allowed me to choose and made financially possible this study (including support from National Research Council grant A-1399).

I thank D.A.M. Craig for many enthusiastic discussions of some of the results of this work. I also express my appreciation to both he and J.S. Nelson for serving on my supervisory committee.

I also express my appreciation to my wife Annette, who shared numerous field trips and has helped with many of the tasks involved in this study.

To my fellow students with whom I have had numerous discussions about the principles and foundations of systematics and about this work, I express my gratitude: in particular S. Ashe, D. Lafontaine, R. Longair, and R. Roughley.

I thank G. Braybrook for technical assistance with the scanning electron microscope and J. Scott for his helpful suggestions concerning drafting techniques and for completing some of the figures. I acknowledge D.E. Griffiths for her masterful drawing of the frontispiece.

I thank all the individuals and institutions listed in Section 2.1 for loan of material.

I express my appreciation to Parks Canada for collecting permits for Jasper and Banff National Parks.

Table of Contents

Chapter		Page
1.	Introduction	1
2.	Materials and Methods	6
	2.1 Materials	6
	2.2 Methods	10
	2.2.1 Collection, Preservation and Dissection of Material	10
	2.2.2 Rearing Methods and Mating Experiments	14
	2.2.3 Adult Feeding Experiments	16
	2.2.4 Measurements and Statistics	17
	2.2.5 Illustrations	23
	2.2.6 Criteria for Species Recognition	24
	2.2.7 Taxonomic Methods	26
	2.2.8 Literature	28
3.	Classification	29
	3.1 Genus *Chaoborus*	29
	3.2 Diagnosis and Description of the Subgenus *Schadonophasma*	33
	3.3 Key to the Species of *Schadonophasma*	37
	3.4 Description of *Chaoborus trivittatus* (Loew)	43
	3.5 Description of *Chaoborus cooki* Saether	62
	3.6 Description of *Chaoborus nyblaei* (Zetterstedt)	74
4.	Analysis of Morphological Variation	83

Chapter		Page
4.1	Artifical Variation	83
4.2	Characters Varying Between Larval Instars	86
4.2.1	Homologous Structures Between First and Later Larval Instars of *Schadonophasma*	88
4.2.2	Head Capsule Length	91
4.2.3	Antennal Length	93
4.2.4	Distance of Antennal Seta From Base of Antenna/Antennal Length (AS/AL)	94
4.2.5	Length of Long Antennal Blade/Antennal Length (LB/AL)	94
4.2.6	Length of Long Antennal Blade/Length of Short Antennal Blade (LB/SB)	94
4.2.7	Postantennal Filaments	96
4.2.8	Prelabral Appendages	96
4.2.9	Number of Mandibular Fan Bristles	97
4.2.10	Anal Fan Setae	97
4.3	Variation of Characters of Fourth Instar Larvae	99
4.3.1	Age-related Variation	99
4.3.2	Sex-associated Variation	101
4.3.2.1	*Chaoborus trivittatus*	101
4.3.2.2	*Chaoborus cooki*	103
4.3.2.3	*Chaborus nyblaei*	108
4.3.3	Correlation of Characters	109
4.3.4	Geographical Variation	111
4.3.4.1	*Chaoborus trivittatus*	112
4.3.4.2	*Chaoborus cooki*	120

Chapter Page

4.3.5 Compound Character Index and Characters Differing Between Fourth Instar Larvae of Species of Schadonophasma 124

4.4 Variation of Characters of Pupae 129

4.5 Variation of Characters of Male Adults 132

4.6 Variation of Characters of Female Adults 137

4.7 Descriptions of Populations Incertae Sedis 140

4.7.1 Sample from Russell Lake, Alberta 141

4.7.2 Sample from Mechant Lake, Quebec 141

4.7.3 Sample from Gallienne Lake, Quebec 143

5. Bionomics and Behavior 148

5.1 Life Cycle 148

5.1.1 Chaoborus trivittatus 150

5.1.2 Chaoborus cooki 152

5.1.3 Chaoborus nyblaei 158

5.2 Development and Behavior 160

5.2.1 Adults 160

5.2.2 Eggs 168

5.2.3 Larvae 171

5.2.4 Pupae 175

6. Mating Experiments 177

7. Phylogeny and Zoogeography 180

7.1 Evidence and Recognition of Three Species of Schadonophasma 182

7.2 Phylogeny of Chaoborus 185

7.3 Fossil Evidence 193

Chapter Page

7.4 Phylogeny of Schadonophasma 195

7.5 Zoogeography and Speciation Events 200

8. Concluding Remarks 205

References 207

Autobiography 271

List of Tables

Table		Page
1	Material other than *Schadonophasma* examined	7
2	Descriptive statistics for male adult *C. trivittatus* ..	45
3	Descriptive statistics for female adult *C. trivittatus*	46
4	Descriptive statistics for male pupae of *C. trivittatus*	47
5	Descriptive statistics for female pupae of *C. trivittatus*	47
6	Descriptive statistics for fourth instar larvae of *C. trivittatus*	48
7	Descriptive statistics for third instar larvae of *C. trivittatus*	48
8	Descriptive statistics for second instar larvae of *C. trivittatus*	50
9	Descriptive statistics for first instar larvae of *C. trivittatus*	50
10	Descriptive statistics for eggs of *C. trivittatus*	51
11	Descriptive statistics for male *C. cooki*	63
12	Descriptive statistics for female *C. cooki*	64
13	Descriptive statistics for male pupae of *C. cooki*	65
14	Descriptive statistics for female pupae of *C. cooki*	65
15	Descriptive statistics for fourth instar larvae of *C. cooki*	66

Table		Page
16	Descriptive statistics for third instar larvae of C. cooki	66
17	Descriptive statistics for second instar larvae of C. cooki	68
18	Descriptive statistics for first instar larvae of C. cooki	68
19	Descriptive statistics for eggs of C. cooki	69
20	Descriptive statistics for male pupae of C. nyblaei	78
21	Descriptive statistics for female pupae of C. nyblaei	78
22	Descriptive statistics for fourth instar larvae of C. nyblaei	79
23	Descriptive statistics for eggs of C. nyblaei	79
24	Comparison of studies of homologies of mandibular structure of larvae of Chaoborus	92
25	Descriptive statistics of male and female fourth instar larval exuviae of C. trivittatus collected 2.4 km. west of Edmonton, Alberta	102
26	Compound character index used to sex fourth instar larvae of C. trivittatus collected 2.4 km. west of Edmonton, Alberta	104
27	Descriptive statistics of male and female fourth instar larval exuviae of C. cooki collected 32 km. west of Edson, Alberta	105

Table		Page
28	Compound character index used to sex fourth instar larvae of C. cooki collected 32 km. west of Edson	106
29	Compound character index used to sex fourth instar larvae of C. cooki collected 1.6 km. south of Jasper	107
30	Variation in head capsule length (in μm) of fourth instar larvae of C. trivittatus in Alberta	113
31	Variation in AS/AL of fourth instar larvae of C. trivittatus in Alberta	113
32	Variation in PAL/PAW of fourth instar larvae of C. trivittatus in Alberta	114
33	Variation in numbers of mandibular fan bristles of fourth instar larvae of C. trivittatus in Alberta	114
34	Variation in AS/AL of fourth instar larvae of C. trivittatus from the west coast of North America	116
35	Variation in LB/SB of fourth instar larvae of C. trivittatus from the west coast of North America	116
36	Variation in PAL/PAW of fourth instar larvae of C. trivittatus from the west coast of North America	117
37	Variation in numbers of mandibular fan bristles of fourth instar larvae of C. trivittatus from the west coast of North America	117

Table		Page
38	Variation in numbers of anal fan setae of fourth instar larvae of C. trivittatus from the west coast of North America	118
39	Variation in head capsule length (in μm) of fourth instar larvae of C. cooki	121
40	Variation in AS/AL of fourth instar larvae of C. cooki	121
41	Variation in numbers of mandibular fan bristles of fourth instar larvae of C. cooki	122
42	Variation in numbers of anal fan setae of fourth instar larvae of C. cooki	122
43	Compound character index used to recognize fourth instar larvae of Chaoborus trivittatus and Chaoborus cooki	125
44	Variation of penis valve length (in μm) of male adult C. trivittatus	135
45	Descriptive statistics for fourth instar larvae of Schadonophasma from Russell Lake, Alberta	142
46	Descriptive statistics for fourth instar larvae of Schadonophasma from Mechant Lake, Quebec	144
47	Descriptive statistics for fourth instar larvae of Schadonophasma from Gallienne Lake, Quebec	145
48	Descriptive statistics for male pupae of Schadonophasma from Gallienne Lake, Quebec	147

Table		Page
49	Descriptive statistics for female pupae of *Schadonophasma* from Gallienne Lake, Quebec	147
50	Number of *C. trivittatus* immatures collected 2.4 km. west of Edmonton, Alberta	151
51	Numbers of pupae resulting from 45 individually reared fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km. west of Edmonton, Alberta	151
52	Records of field collected adult *C. trivittatus* from southern Ontario and Quebec and northeastern United States	153
53	Numbers of *C. cooki* immatures collected 1.6 km. south of Jasper, Alberta	155
54	Numbers of *C. cooki* immatures collected 32 km. west of Edson, Alberta	156
55	Numbers of *C. cooki* immatures collected 1.4 km. west of George Lake, Alberta	157
56	Life span of chaoborid species previously reported	162
57	Numbers of pupae resulting from 42 individually reared fourth instar larvae of *C. cooki* collected 32 km. west of Edson, Alberta	174
58	Results of intraspecific and interspecific crossings of adult *C. trivittatus* and *C. cooki*	178
59	Characters and character states within the genus *Chaoborus*	187

Table Page

60 Characters and character states within the subgenus Schadonophasma 196

List of Figures

Figure		Page
1	Place names in Alberta cited in text	232
2	A. Characters and measurements of head capsule of fourth instar larva. B. Characters of terminal abdominal segments of fourth instar larva. C. Terminalia of male pupa. D. Terminalia of female pupa	233
3	Terms and measurements of A. Terminal abdominal segments of pupa. B. Male adult penis valve. C. Wing of adult (male)	234
4	A. Third tarsomere of female adult. B. Microsculpture of head capsule of fourth instar larva. C. Exochorion of egg of *Chaoborus trivittatus*. D. Exochorion of egg of *Chaoborus cooki*	235
5	Posture of live pupae. A. *Chaoborus cooki*. B. *Chaoborus trivittatus*	236
6	Abdominal chaetotaxy of pupa of *Schadonophasma*	237
7	Antennae and dorsal outline of head capsule of larval instars of *Schadonophasma*	238
8	A. Mandible of first instar larva. B. Mandible of fourth instar larva. C. Dorsal process of fourth instar larva of *Chaoborus nyblaei*. D. Terminal abdominal segments of fourth instar larva of *Chaoborus cooki* showing position of tracheae	239
9	Egg structure. A. *Chaoborus trivittatus*. B. *Chaoborus nyblaei*. C. *Chaoborus cooki*. Egg shell.	

Figure		Page
	D. Chaoborus trivittatus. E. Chaoborus cooki	240
10	Penis valves of adult male Chaoborus trivittatus	241
11	Penis valves of adult male Chaoborus cooki and Chaoborus nyblaei	242
12	Variation of penis valves of adult males due to orientation. A-E. Chaoborus trivittatus. F-J. Chaoborus cooki	243
13	Prelabral appendages of fourth instar larvae of Chaoborus trivittatus	244
14	Prelabral appendages of fourth instar larvae of Chaoborus cooki	245
15	Prelabral appendages of fourth instar larvae of Chaoborus nyblaei	246
16	Known distribution of Chaoborus trivittatus	247
17	Known distribution of Chaoborus trivittatus in Alberta	248
18	Known distribution of Chaoborus cooki	249
19	Known distribution of Chaoborus cooki in Alberta	250
20	Known distribution of Chaoborus nyblaei	251
21	Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. Head capsule length. B. Antennal length	252
22	Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. AS/AL. B. LB/AL	253

Figure Page

23 Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. LB/SB. B. Postantennal filament length 254

24 Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki A. PAL/PAW B. Number of mandibular fan bristles 255

25 Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki A. Number of anal fan setae. B. Temporal distribution of fourth instar larvae of Chaoborus trivittatus and Chaoborus cooki 256

26 Age-related variation of male fourth instar larvae of Chaoborus cooki. A. Relationship between total length and long antennal blade length. B. Relationship between total length and prelabral appendage length 257

27 Results of compound character index used to sex fourth instar larvae. A. Of Chaoborus trivittatus from 2.4 km. west of Edmonton, Alberta. B. Of Chaoborus cooki from 32 km. west of Edson, Alberta. C. Of Chaoborus cooki from 1.6 km. south of Jasper 258

28 Correlation of characters of fourth instar larvae A. Male Chaoborus trivittatus. B. Female Chaoborus trivittatus. C. Male Chaoborus cooki. D. Female Chaoborus cooki 259

Figure		Page
29	Relationship between antennal length and distance of antennal seta from base of antenna of fourth instar larvae. A. Chaoborus trivittatus. B. Chaoborus cooki. C. Chaoborus nyblaei	260
30	Localities of samples used to study geographical variation of characters of fourth instar larvae of Chaoborus trivittatus in Alberta	261
31	Localities of samples used to study geographical variation of characters of fourth instar larvae of Chaoborus trivittatus from the west coast of North America	262
32	Localities of samples used to study geographical variation of characters of fourth instar larvae of Chaoborus cooki in Alberta	263
33	Results of compound character index used to recognize fourth instar larvae of Chaoborus trivittatus and Chaoborus cooki	264
34	Variation of characters of fourth instar larvae of Chaoborus trivittatus. A. Number of mandibular fan bristles. B. LB/SB. C. LB/AL	265
35	Mortality of adult Chaoborus trivittatus. A. Males. B. Females	266
36	Phylogeny of species of Chaoborus	267
37	Relationship between number of anal fan setae and head capsule length of fourth instar larvae of Chaoborus species	268

Figure | Page

38 Phylogeny of species of Schadonophasma 269

39 Schematic representation of events of sympatric speciation of lineages giving rise to Chaoborus trivittatus and Chaoborus cooki-nyblaei 270

1. Introduction

For systematists interested in understanding the intraspecific and interspecific variation of species, a common concern is the investigation of species which do not exhibit discrete morphological characteristics allowing identification of individuals. This study is partially an investigation of such a problem within the genus Chaoborus Lichtenstein. I first recognized that it was difficult to separate species of the subgenus Schadonophasma Dyar and Shannon, while attempting to identify fourth instar larvae, pupae and adults using Saether's (1972) key. Some specimens exhibited combinations of characters from different species as delimited by Saether (1970, 1972). I therefore undertook a reinterpretation of variation exhibited by members of this subgenus through examination of the structural and bionomic features of eggs, all stages of larvae, pupae and adults.

Although Chaoborus is composed of species with marked variation which show slight morphological differences between species, few studies have attempted to precisely interpret this variation. Saether (1967) showed that the characters previously thought to separate C. flavicans (Meigen) and C. alpinus Peus feature overlapping variation and consequently he considered these forms to be conspecific. However, overlap of variation alone is not evidence of reproductive unity. Detailed analysis of character variation, distributional data

and bionomic information yield superior criteria from which to decide species status. I have incorporated all these criteria into the following study.

However, criteria allowing recognition of members of different species is only the initial step permitting systematists to investigate species. I therefore further undertook study of intraspecific variation of the species, including analysis of sex-associated, age-related and geographical variation, and differences between larval instars. Sources of variation of individual characters of Chaoborus species are not well understood. Sikorowa (1973) showed that some variation of C. flavicans can be considered ecotypic and Cook (1956:32) suggested the same for C. punctipennis (Say) larvae. Variation in number of mandibular fan bristles, ratio of length to width of prelabral appendages, total length (Smith, 1960a:398) and air sac length (von Frankenberg, 1915:514) of fourth instar C. crystallinus (De Geer) larvae is sex-associated. Total length and color of C. americanus (Johannsen) fourth instar larvae is also sex-associated (Bradshaw, 1973:1249) as well as reflecting a polymorphism. Roth (1967:66) noted worn prelabral appendages of overwintered fourth instar larvae of C. albatus Johnson. Seasonal differences of total length of mature fourth instar larvae of C. punctipennis was reported by Muttkowski (1918:407). C. punctipennis adult size (Cook, 1956:32) and number of mandibular fan bristles of C. anomalus Edwards fourth instar larvae (McGowan, 1972:365) may vary geographically. All these studies suggest possible sources of variation and I have attempted to provide interpretations of variation of characters of species of Schadonophasma also in the light of these previous studies.

Systematic studies should be based on evolutionary theory and the aforementioned analyses provide a sufficient background from which to hypothesize the evolutionary history of the subgenus Schadonophasma and to also propose a possible example of sympatric speciation. An interpretation of the phylogeny of some Chaoborus species is provided.

Because of their importance as fish food (Goldspink and Scott, 1971; Green et al., 1973; Kruger, 1973; Lindquist et al., 1943; MacDonald, 1956; Pope et al., 1973), as mosquito predators (Montchadsky, 1964; Sailer and Lienk, 1954; Skierska, 1969, 1974), in the prominent role they play in fresh water communities (e.g. Bonomi, 1962; Fedorenko and Swift, 1972; Juday, 1921; Miyadi, 1932; Miyadi and Hazema, 1932; Petr, 1972; Swüste et al., 1973; Woodmansee and Grantham, 1961) and occasionally as pests (Brydon, 1956; Herms, 1937; Hitchcock, 1965; Lindquist and Deonier, 1942a, 1942b; Lindquist et al., 1951; Donald, 1953, 1956; Shemanchuk, 1959) many Chaoborus populations are better understood bionomically than systematically. For example, although C. flavicans has been studied ecologically in detail (e.g. Parma, 1971b; Balvay, 1977d), no thorough distributional study has been done on this species or any other species of the Holarctic region. This situation allows systematists working on Chaoborus to take into account a wide array of ecological work and to draw systematic inferences from such studies.

Chaoborus is composed of medium sized flies 2.0-8.5 mm. in length. Adults of this genus are not known to bite although the most primitive genus of the family, Corethrella Coquillett, includes species with haematophagous adults (Miyagi, 1974, 1975; Williams and Edman, 1968). In the Holarctic region larvae may be commonly found in permanent and temporary lentic waters and occasionally in rivers.

Chaoborus includes 35 described species in six subgenera (Neochaoborus Edwards, Sayomyia Coquillett, Edwardsops Lane, Peusomyia Saether, Schadonophasma, and Chaoborus s. str.). The genus has been recorded from most major land masses with the exception of New Zealand, Antarctica, Greenland, and most oceanic islands. Edwards (1932) gave a world list of species and their distribution. The Palaearctic species have been described most recently by Hirvenoja (1961), Martini (1931), Parma (1969), Peus (1934), Prokesova (1959), and Sikorowa (1967a, 1973) and Nearctic species by Dyar and Shannon (1924) and Cook (1956) who also provided a detailed morphological study. Saether (1970) gave the most recent revision of Palaearctic and Nearctic species and was first to compare material of most species from both these regions. Palaearctic and Nearctic samples of C. flavicans were studied by Saether (1967). Saether (1972) presented keys to fourth instar larvae, pupae and adults of species of the Holarctic region and gave a synopsis of their way of life and structure.

Lane (1953) and Saether (1976) have provided descriptions for most known species of Chaoborus in South America. African species have been described by Edwards (1930), Green and Young (1976), McGowan (1972, 1976), and Verbeke (1957, 1958) and Oriental and Australian species by Giles (1902, 1904), and Theobald (1901b, 1903). Fossil species have been described by Edwards (1923), von Heyden (1862), Meunier (1904), and Scudder (1890; questionable identification).

The objects of this study were species of the subgenus Schadonophasma, whose adults and larvae are the largest of Chaoborus species. Species are restricted to northern boreal regions. Larvae

of all species sometimes occur in large numbers in permanent and temporary lentic waters. Adults and immatures are poorly represented in museum collections.

Most descriptions are brief and bionomic information anecdotal (Allan, 1973; Anderson and Raasveldt, 1974; Dickenson, 1944; Dodson, 1970; Dyar and Shannon, 1924; Edwards, 1932; Felt, 1904, 1905; Giles, 1902; Hamilton, 1971; James et al., 1969; James and Smith, 1958; Jenkins and Knight, 1950; Johannsen, 1903, 1934; Loew, 1862; Matheson, 1944, 1945; Pope et al., 1973; Smith, 1960b; Theobald, 1901b; Tulloch, 1934; Twinn et al., 1948; Zetterstedt, 1838, 1851). The feeding characteristics and vertical migration of the larvae and the life cycle of C. trivittatus (Loew) from Eunice Lake, British Columbia have been described by Fedorenko (1975a, 1975b, 1975c), Fedorenko and Swift (1972), Swift (1975, 1976), and Swift and Fedorenko (1975).

Schadonophasma was erected as a subgenus by Dyar and Shannon (1924) to contain the North American species C. trivittatus. Edwards (1932), Cook (1956), Matheson (1944), and Peus (1967) considered C. nyblaei (Zetterstedt) to be conspecific with C. trivittatus. Hirvenoja (1961), however, concluded these to be two distinct species. Saether (1970) recognized on morphological grounds C. nyblaei in Fennoscandia and Baffin Island, Canada, and C. trivittatus, C. cooki Saether and C. brunskilli Saether in North America. This study clarifies the confusion presented by the work of the above authors concerning the species of Schadonophasma.

2. Materials and Methods

2.1 Materials

This study was based on examination of 293 eggs of C. cooki, more than 50 egg masses of C. trivittatus, and of all other species, 49 first instar, 58 second instar, 139 third instar, and 832 fourth instar larvae, 93 and 80 female pupae or pupal exuviae and 311 male and 248 female adults. Eggs and most adults were preserved in fluid and members of other stages and some adults were mounted on microscope slides. Many more specimens of all stages, preserved in fluid, were studied. All Schadonophasma material examined by Saether (1970), except the male pupa of C. trivittatus, was reexamined. I have also examined material collected by Osten Sacken (MCZ) but, because I could not interpret the locality labels, did not include the material in this study.

For comparative purposes I also examined various stages of other species of Chaoborus, Mochlonyx Loew, and Eucorethra Underwood (Table 1).

Because I wanted to sample a wide geographical area and sampling lakes would have taken too much time, I collected immatures only from smaller water bodies and depended on loans for material from lakes. Place names in Alberta referred to in the text are indicated in Figure 1.

Voucher specimens from this study and some of the material I collected are in the Strickland Museum, Department of Entomology,

Table 1. Material other than Schadonophasma examined.

	First Instar	Second Instar	Third Instar	Fourth Instar	Pupae	Adults
C. americanus		X	X	X	X	X
C. crystallinus		X	X	X	X	X
C. flavicans	X	X	X	X	X	X
C. obscuripes			X			
C. punctipennis				X	X	X
C. albatus				X		X
C. pallidipes		X	X	X		
C. anomalus		X	X	X		
C. ceratopogones		X	X	X		
M. fuliginosus	X	X	X	X		
M. velutinus			X	X	X	X
E. underwoodi	X	X	X	X	X	X

University of Alberta, Canada. Other material collected is deposited in museums as indicated in the list of localities at the end of species descriptions.

Nearly all immatures and about half of all adults were collected by myself, mostly in Alberta. The remainder was borrowed from the following museums or persons designated in the text by the following abbreviations. Names of curators are also given to facilitate inquiries about their collections.

ABOr - A. Borkent, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3.

BMNH - British Museum (Natural History), London, England, SW7 5BD; P.S. Cranston.

CAS - California Academy of Sciences, San Francisco, California, USA, 94118; P.H. Arnaud.

CNC - Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario, K1A 0C6; D.M. Wood.

CUNY - Department of Entomology, Cornell University, Ithaca, New York, USA, 14850; L.L. Pechuman.

EFCo - E.F. Cook, Department of Entomology, Fisheries and Wildlife, St. Paul, Minnesota, USA, 55101.

FWI - Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, Canada, R3T 2N6; D.M. Rosenberg.

JDAl - J.D. Allan, Department of Zoology, University of Maryland, College Park, Maryland, USA, 20742.

MCZ - Museum of Comparative Zoology, Cambridge, Massachusetts, USA, 02138; J.F. Lawrence

OASa - O.A. Saether, Museum of Zoology, University of Bergen, N-5014 Bergen, Norway.

UASM - Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3; G.E. Ball.

USNM - Systematic Entomology Laboratory, United States Department of Agriculture, c/o United States National Museum, NHB 168, Washington, D.C. USA, 20560; C.F. Thompson.

WSUP - Department of Entomology, Washington State University, Pullman, Washington, USA, 99163; W.J. Turner.

ZMHF - Zoological Museum, Division of Entomology, SF-00100, Helsinki 10, Finland; B. Lindeberg.

ZMLS - Zoological Institute, Department of Systematics, Helgonavägen 3, S-223 62 Lund, Sweden; H. Andersson.

2.2 Methods

2.2.1 Collection, Preservation and Dissection of Material

Egg masses of C. trivittatus, like those of most other Chaoborus species, float at the surface of the water body in which they are laid. I collected these by hand picking the floating masses from the water surface with soft-tipped tweezers and dropping them into 70% ethanol. Although egg masses can be scooped from the water surface with a dip net, they stick to the netting and attempts then made to pick them up result in their disintegration. This method should be avoided if determinations of the number of eggs per egg mass are important.

Because Schadonophasma larvae concentrate in the shaded portions of ponds such as that provided by Typha, surrounding trees, or willows, it is imperative that these areas be sampled. A common method of collecting larvae is to briskly sweep an aquatic net through a water body. Many third and fourth instar larvae are benthic during daylight hours, so stirring up the bottom is important to insure adequate samples of these stages.

First and second instar larvae, because of their small size, are best collected with a plankton net. In this study only ponds were sampled so that the plankton net, with a mesh size of 116 µm, was thrown from the shore and hauled in. Contents of either aquatic or plankton net were washed out in a white enamel pan with three to five cm. of water to insure that all captured specimens were retrieved. The immatures were then picked up with soft-tipped

tweezers and dropped into 70% ethanol.

Pupae are collected in the same manner as larvae except that an overly brisk motion of either plankton or aquatic net will result in specimens in which the pupal horns have been lost. Pupal exuviae are commonly found on the leeward side of ponds and can be collected by hand or aquatic net.

Adults were sampled by means of an aerial net. Females of C. trivittatus are sedentary and although they can occasionally be collected with an aerial net, are best retrieved with an aspirator from tree trunks and herbaceous plants at the periphery of ponds.

I attempted to collect adult Schadonophasma with light traps but with little success. Examination of all the material collected by 22 New Jersey light traps (60 watt incandescent bulbs) in and around Edmonton, Alberta from June 24 to September 4, 1974 yielded only two female C. cooki. These traps, run by City of Edmonton, Mosquito Control, did yield 1065 adults of Chaoborus s. str.. I ran a New Jersey and CDC (Communicable Disease Center) light trap beside a pond from which C. cooki adults were emerging with no success.

Quantitative samplings of immatures necessary for life cycle studies were obtained with the plankton net which was thrown out at least six times in the same direction from the shore and dragged at least twice across the bottom, resulting in the bottom being disturbed and thereby insuring a representative sample. The numbers of immatures in each sample were not meant to be temporally comparable but were interpreted to reflect only percentages of an instar present at a given time.

Material, with the exception of some pinned adults, was preserved in 70% ethanol. However, retention in alcohol for long periods of time will lighten the pigmentation of specimens. Pinned specimens are prerequisite for estimation of adult coloration.

All immatures to be measured were prepared using the method described by Saether (1972) with the following modifications. Specimens were not cleared in KOH as this is not necessary for accurate measuring or examination and clearing has resulted in some faulty observations concerning shape of the dorsal process of larvae. One antenna and both mandibles were removed from each larva while in Canada Balsam to insure retention of these parts, especially of younger instars whose mouthparts are easily lost. All larvae were mounted laterally and all pupae and pupal exuviae were mounted with their ventral surfaces up. Pupal exuviae should be mounted with glass chips to support the coverslip to prevent compression of the specimen. An alternative method is to mount the specimen in Canada Balsam which is then allowed to dry for a few hours before application of the coverslip.

Schlee (1966) indicated the advantages of fluid preserved material for the examination of chironomid adults. Mainly, dried material results in distortion of some key characters. As can be expected, this is also true of chaoborid adults. Therefore, material which was to be examined in detail was mounted in Canada Balsam. The two antennae, head, thorax, three left legs, wings and abdomen were disarticulated. Heads, thoraces, and abdomens were cleared in

hot 8% KOH, transferred to 15% acetic acid for 15 minutes, and all parts treated consecutively for at least 10 minutes each with 98% ethanol, 98% ethanol layered over cedarwood oil, cedarwood oil and Canada Balsam. Chaoborus adults need not be so treated to be identified. Most adult material examined was pinned.

The abdomen of each pinned male, after clearing in hot 8% KOH, was placed in one of eight arbitrarily numbered wells filled with glycerine on each of a number of 7.6x7.6 cm. microscope slides and examined under both stereoscopic and compound microscopes. This insured that no a priori decisions were made concerning species differences. Maximum lengths of the penis valves were estimated with the aid of the compound microscope at 200X magnification. After examination, abdomens were stored in glycerine in a genitalia vial on the pin. Examination of the genitalia from different orientations is imperative for the determination of interspecific differences of the penis valve.

Abdomens of some pinned females were treated with a weak solution (three to six crystals in three drams of distilled water) of tri-sodium orthophosphate. This treatment restores dried, more or less shrivelled parts to approximately natural size and also restores eggs, if present in the abdomen, to their natural dimensions.

Number of eggs per female was determined using reared specimens killed in 70% ethanol. Eggs were easily removed and counted while in this medium.

2.2.2 Rearing Methods and Mating Experiments

All live material was reared at 20°C and a long day (18:6, light:dark) photocycle. Field collected cladocerans, copepods and chironomid larvae and lab reared larvae of Culiseta inornata provided a continual food source for the larvae. Rearings of larvae to pupae were completed with each larva in a separate Dominion Brand 473 ml. wide mouthed Mason jar filled with pond water to insure that no larvae were lost due to cannibalism.

To determine length of pupal period, larvae were reared to adulthood in a 22.7 liter aquarium filled with pond water and an abundance of food. Pupae were removed on the day they appeared and kept in separate Mason jars.

In general, rearings were completed from field collected fourth instar larvae, although earlier instars were occasionally captured for rearing. Pupae were not used for rearings as capture often resulted in at least one pupal horn being broken off and consequently, a reduced adult emergence (Parma 1971b:46; pers. obs.).

Adults could not be made to mate successfully in the lab except when decapitated males were brought into contact with CO_2 anesthetized females, the method used for mating experiments. Adults were reared from fourth instar larvae of C. trivittatus collected at 2.4 km. west of Edmonton, Alberta on 13-V-1976 and 16 km. west of Jasper, Alberta on 18-V-1976 and C. cooki collected 1.4 km. west of George Lake, Alberta on 13-V-1976. After mating, each female was placed in a three dram vial with wet paper towelling and gauze was placed over the mouth of the vial. Few adults were used in these

experiments because of the difficulty in synchronizing adult emergence of C. cooki and C. trivittatus in the laboratory. For the purposes of this study only eggs which embryonated were considered fertilized.

2.2.3 Adult Feeding Experiments

This experiment had two purposes; first, to see if adult C. trivittatus drink water and second, to determine if water uptake affects longevity. Goff (1972) tested for imbibition of water by adults of Chironomus riparius by coloring sucrose water with food coloring and checking excreta for color changes. This method was used with C. trivittatus adults to determine if imbibition of water took place.

Adult C. trivittatus were collected at 1500-1600 h on May 6, 1976, 2.4 km. west of Edmonton, Alberta, with an aerial net and aspirator. They were transported to the laboratory in a screened cage placed in a styrofoam container with wet paper towels. The adults were then anaesthesized with CO_2 and sorted into treatments by 2300 h on the day of capture. Ten males were placed in each of 15 mason jars and four females in each of three jars. All were kept at 20° C with a long day (18:6, L:D) photocycle. Each jar contained a 35X10 mm. plastic petri dish containing 5 ml. of deionized water which was either 1) clear and available 2) 1% blue food coloring solution (Scott Bathgate Ltd., Winnipeg, Toronto, Vancouver; 'Food Club' color kit) and available or 3) screened with netting to prevent the flies from drinking. I assumed uniform humidity in all jars. Fifty males and four females were used in each treatment. The low numbers of females used was due to their scarcity in the field.

Mortality and the presence or absence of colored excreta was recorded every 12 hours. Some specimens were lost during the experiment and the covered water spilt in one jar, so that these ten males were not included in the experiment.

2.2.4 Measurements and Statistics

All measured specimens are listed at the end of species descriptions. Most measurements were made with an ocular micrometer (120 divisions) through a Wild M20 compound microscope equipped with phase contrast. Total length of larvae and the Y/X wing ratio were measured with an ocular micrometer (120 divisions) through a Wild M5 stereoscopic microscope. Measurements were taken at as high a magnification as was practical to comply as far as possible with Sokal and Rohlf's (1969:15) suggestion that there be 30 to 300 units of measurement between minimum and maximum values.

Terms for structures follow those used by Cook (1956), Knight (1971a, 1971b) or Laffoon and Knight (1971). It is likely that many structures of Chaoborus larvae are homologous to those of culicid larvae. For example, what are termed here antennal seta and antennal blades are probably homologous to the antennal setae of culicid larvae (Knight and Laffoon, 1971). However, until detailed comparative studies are completed, I use the traditional terms.

Measurements of larval structures were those recognized as taxonomically useful by Cook (1956), Parma (1969), Saether (1970) and Sikorowa (1973). Although numbers of bristles in both mandibular fans were counted, to reduce the consequences of possibly lost bristles, only the highest number was used for analysis. Total length was measured as length of head capsule plus distance from the anterior edge of the prothorax to the tip of the abdomen exclusive of the anal tubules. Anal fan setae which are broken off at the bases can

still be counted by noting the internal portion of the setae. Some anal fan setae of some larvae were reduced as compared to the other setae and these were only counted if they were at least 0.5 as long as the longest anal fan seta. I attempted to study the chaetotaxy of larvae but found most setae too difficult to see to obtain reliable, comparative results. I did not study the shape of anal tubules. Studies by Wichard (1975) and Wigglesworth (1933, 1965) would suggest that these would exhibit too large a degree of variation to be useful in distinguishing the morphologically similar species of Schadonophasma.

Measurement of pupal features follows the treatment by Saether (1970). Pupal abdominal length was measured from the anterior margin of abdominal tergite I to the posterior margin of abdominal segment VIII. I found total length to be too difficult to measure accurately from slide mounted material.

Saether (1970) recorded 74 measurements and 20 ratios from males and 67 measurements and 15 ratios from females of adult C. cooki (♂,n=7; ♀ ,n=4) and C. trivittatus (♂,n=7; ♀ n=5). According to the results of this study these were all, with the possible exception of the adult male C. trivittatus from Lac Phillipe, Quebec, correctly identified. Those measurements or ratios judged, on the basis of Saether's study, to be of possible taxonomic use were studied from slide material. Two of the most important characters, penis valve shape and Y/X wing ratio were also studied from pinned material. Terms for structures of the penis valves are shown in Figure 3B. Total length of the penis valve was measured from the base of the penis valve to the tip of the claw. The characterization of penis valves was based on a study of these structures from many orientations. Because it was impossible to standardize these, future

comparisons must be based on orientations in which the penis valves look similar to those illustrated in this work.

All thoracic setae, except scutellar setae, of the adults were counted on one side of the thorax. Setae on tergite IX were counted for only one side.

Searches for additional characters of all stages to separate the species of Schadonophasma, except eggs, previously undescribed, were generally fruitless. Features which yielded no criteria for separation of the species were:

Adults. Structure of digestive tract; setal pattern on thorax; extent of coloration; sperm shape.

Male and female pupae. Reticulation of pupal horns; length/width of respiratory horn; chaetotaxy of abdominal segments II-VIII; coloration, including that of the ribs of the anal paddle; anal paddle shape; degree of serration of outer rib of paddles; length of median rib; distance of plumose seta from base of median rib; distance of plumose seta from base of median rib/length of median rib; length, width, and length/width of genital lobes.

Fourth instar larvae. Microsculpture of head capsule; dorsal outline of head capsule; shape of antennae; curvature of long antennal blades; length of postantennal filaments; length of labrum; width of labrum; distance of long seta from anterior base of labrum; ratio of the distance of long seta from anterior base of labrum to the length of labrum; shape of maxillae; length of seta on maxillary palpus; lateral outline of the dorsal process.

I assumed that characters, with the exception of the length of the postantennal filaments, not useful for identification of fourth instar larvae would not be useful for younger instars.

Ratios were used to describe shapes or proportions statistically and are complemented by illustrations. Measurements used to construct ratios or ratios themselves are abbreviated as follows.

Adults - X = length of vein Rs between R-M and fork of Rsa and Rs (Fig. 3C)

Y = length of vein Rs between R-M and fork of R_2 and R_3 (Fig. 3C)

Z = length of vein M between R-M and fork of M_1 and M_2 (Fig. 3C)

R_3 = length of vein R_3 (Fig. 3C)

M_1 = length of vein M_1 (Fig. 3C)

Fe= femur length

Ti= tibia length

Ta_1-Ta_5= length of tarsomeres 1-5

$\frac{L}{R} = \frac{\text{length of first tarsomere}}{\text{length of tibia}}$

$\frac{P}{U} = \frac{\text{length of penultimate antennal article}}{\text{length of ultimate antennal article}}$

$\frac{HW}{PL} = \frac{\text{head width}}{\text{prementum length}}$

$HV = \frac{\text{length of male}}{\text{dististyle length X 10}}$

$HR = \frac{\text{Basistyle length}}{\text{Dististyle length}}$

Male and Female Pupae -

$\frac{WS}{LS} = \frac{\text{width of seventh abdominal segment}}{\text{length of seventh abdominal segment}}$ (Fig. 3A)

Larvae - $\frac{AS}{AL} = \frac{\text{distance of antennal seta from base of antenna}}{\text{antennal length}}$ (Fig. 2A)

$\frac{LB}{AL} = \frac{\text{length of long antennal blade}}{\text{antennal length}}$ (Fig. 2A)

$\frac{LB}{SB} = \frac{\text{length of long antennal blade}}{\text{length of short antennal blade}}$ (Fig. 2A)

$\frac{PAL}{PAW} = \frac{\text{prelabral appendage length}}{\text{prelabral appendage width}}$ (Fig. 2A)

Legs are referred to by the following abbreviations.

P_1 = foreleg

P_2 = midleg

P_3 = hindleg

Statistical tests were used to compare species, larval instars and sexes, to understand geographical variation and to complement the species descriptions. Descriptive statistics of samples of eight or more individuals are ranges, means, 1.5 standard deviations (SD), and two standard errors (SE) each side of the mean. For samples of less than eight, only range and mean are given. Ranges only are given for samples of two. Total length of larvae is expressed only as a range because it is growth related and for the purposes of this study, further statistics would not give additional information.

Because Schadonophasma fourth instar larvae could not be identified on the basis of discrete characters, I employed a compound character index to recognize fourth instar larvae of C. trivittatus and C. cooki. Although this index has been used primarily to recognize hybrids and analyze zones of hybridization (Freitag, 1965, and papers citied therein; Hubbs and Peden, 1969, Rising, 1970) it is also useful to distinguish morphologically similar species. Compound character indices compile an overall measure of difference to test for morphological discontinuity (i.e. reproductive isolation). Kim et al. (1966) have given a step by step analysis of how characters are best used in combination to distinguish similar species and I have followed most of their suggestions. However, because I was using the index to test for lack or presence of conspecificity of samples and provide a means of identification, I did not statistically test homogeneity

of samples and could not determine, beforehand, the amount of overlap of character variation between species.

Differences between male and female larvae and pupae were estimated using the unpaired T-test.

2.2.5 Illustrations

All illustrations were made with the aid of a drawing tube on a Wild M20 compound microscope from slide mounted material. They complement verbal or statistical descriptions of the species and describe the complex shape and depict the various forms of adult penis valves. Shape of the lateral outline of the dorsal process is also described with illustrations. Penis valves were drawn with the head in a horizontal plane.

Scales on figures represent 0.1 millimeter unless otherwise stated.

Scanning electron photomicrographs give a visual impression of some characters.

Distribution maps are provided. Dots represent collecting sites of all stages of a species. These localities are a composite of all material examined and therefore may not accurately reflect present distributions. Details of collecting sites and dates, and stage collected of measured specimens are available at the end of each species description.

2.2.6 Criteria for Species Recognition

I have accepted for the purposes of this study Mayr's (1969) species definition as 'groups of actually (or potentially) interbreeding populations which are reproductively isolated from other such groups'. Reproductive isolation may be reflected in discontinuities in the variation of characters and especially in circumstances of sympatry, be used to recognize species. However, some discontinuities can be better explained by other interpretations. Circles of races, ecophenotypic or polymorphic variation may be interpreted incorrectly as reflecting barriers to gene flow and the presences of more than one species (Brown, 1959; Mayr, 1969; Ross, 1974).

When I initiated this study I suspected that C. trivittatus and C. cooki might be conspecific. I therefore undertook a study of the structure, bionomics, behavior, and development of both species and used these data as criteria for species recognition. In addition, I carried out mating experiments of adults of C. trivittatus and C. cooki. Because of this concordant evidence I was better able to interpret discontinuities of morphological variation.

Lack of bionomic data and associated adults for several samples of immatures made me uncertain of their specific status. I describe and discuss these under the heading 'populations incertae sedis' to better define and encourage further work on the problems posed by these samples.

Although I recognized the subspecies category as useful for the recognition of some distinctive populations, the varied use of

this category has led to numerous misunderstandings of variation within species and I therefore prefer to describe variation of populations without formally classifying them.

2.2.7 Taxonomic Methods

The structure of fourth instar larvae, pupae and adults of several populations of Schadonophasma in Alberta indicated that these were referable to previously described C. trivittatus and C. cooki. Mating experiments and study of behavior and bionomics were used to test interpretation of morphological differences as a result of reproductive discontinuities. Study of such differences was then applied to all available material to determine if these would support indications of lack of conspecificity. A compound character index was used to test for morphological discontinuities of fourth instar larvae of Schadonophasma and provided a means of identification of these larvae. Identification of eggs and first, second and third instar larvae was based on either laboratory rearings or association with identified later stages.

The limited material of C. nyblaei available from Europe presented some problems of interpretation and although the criterion for recognizing this as a sample of a distinct species was mostly morphological, the interpretation of the functional significance of some morphological features supported such a decision.

Geographical variation was studied for two purposes. One was to test my concepts of biological species and the other to better understand the extreme variation and evolutionary history of the species.

Paucity of material limited the stages for geographical variation of characters to fourth instar larvae and adults.

For the study of geographical variation of characters the most informative statistic is the mean. To investigate patterns of variation I plotted mean values of a character for all samples which contained eight or more individuals, on a map of North America or Alberta and visually judged if any patterns were present. Samples of less than eight were lumped with the geographically closest sample.

The geographical variation of all characters of the fourth instar larvae used in the compound character index, of the penis valve length and number of setae on tergum IX of the male adults and for Y/X wing ratio of both male and female adults was studied in detail. Male and female adults were analyzed separately.

The correct naming of taxa was confirmed by examination of types.

I discuss my approach to the evolutionary history of species of Schadonophasma in the section on phylogeny and zoogeography.

2.2.8 Literature

Using the very complete bibliography dealing with Chaoborus compiled by Roth and Parma (1970) as a basis, I attempted to trace every published account of species of Schadonophasma up to at least September, 1977. Because of a rather sparse literature, citations cover every publication I could attribute to a species of Schadonophasma.

Because so much ecological work is dependent on correct recognition of the species studied, I have attempted to reidentify every published record either by examination of the original material or on the basis of published distributional and ecological information.

3. Classification

3.1 Genus Chaoborus

Edwards (1932) gave a complete list of generic synonyms and Cook (1956) and Saether (1972) described the general structure of Chaoborus species. Only additions and corrections to those descriptions are given here. The first, second and third instar larvae are fully described as they differ from fourth instar larvae. Within a species, earlier instars differ from later instars in numerous varying characteristics such as head capsule length, antennal length, postantennal filament length, number of mandibular fan bristles, and number of anal fan setae and these are described for Schadonophasma larvae in a later section. Only qualitative or non-varying differences are described here. Descriptions of earlier instars of Chaoborus species are given by Deonier (1943), McGowan (1972), Parma (1969, 1971a), Prokesova (1959), Saether (1967, 1970), Sikorowa (1973), and Smith (1960a). Eggs or egg masses have been described by Aitken (1954), Berg (1937), Herms (1937), Lindquist and Deonier (1942b), MacDonald (1956), McGowan (1974, 1975, 1976), Parma (1971b), Sikorowa (1973), Smith (1960a) and von Frankenberg (1937).

Saether's comments on the subgenus Sayomyia appear to be based on only the North American species C. punctipennis, C. astictopus Dyar and Shannon, C. albatus, C. annulatus Cook, and C. maculipes

Stone and do not apply to at least some Southern Hemisphere species. Saether's (1970) calculation of HR was incorrect and actually is the inverse of the data he presented.

Some erroneous interpretations of characters differing between larval instars are discussed under the heading 'Characters Varying Between Larval Instars'.

Keys to subgenera of Chaoborus of the Holarctic region for adults, pupae, and fourth instar larvae have been provided by Saether (1972). More comprehensive keys must await analysis of species of the Neotropical, Oriental, and Australian regions. Some corrections to Saether's (1972) keys are presented below in the key to species.

Diagnosis

Adults. Second tarsal article shorter than first; claws on legs of male equal in length; tarsal claws not toothed; females with three seminal capsules; vein R_1 terminated distal to level of apex of vein Cu_1.

Pupae. Respiratory horns with spiracular openings small and slit-like; paddles free, movable and each supported by two marginal and one medial rib (Fig. 2C,D).

Larvae (all instars). Head capsule laterally compressed; antennae proximate; pair of air sacs in both thorax and abdominal segment VII; no respiratory siphon; anal segment with ventral setal fan.

Description of Chaoborus

Adults. females with row of comb-like setae on anterior face of third tarsus of midlegs (Fig. 4A).

Pupae. Respiratory horns spindle shaped (Saether, 1972:272) to globular (Verbeke, 1957:190); terminalia almost parallel (Fig. 5A; Blanchard, 1905:39; Deckart, 1958:269; Prashad, 1918:19; Senior-White, 1927:65; Wesenberg-Lund, 1943:418) to perpendicular (Fig. 5B) to longitudinal axis of body.

Fourth Instar Larvae. Length 4.4-20.3 mm.; predaceous; developing adult eye visible (present or absent in C. anomalus); apex of antenna with six terminal setae (Fig. 2A), four long, one distinctly shorter, one much shorter; pair of setae dorso-posterior to antennae dendritic; 10 postantennal filaments; prelabral appendages one in front of other, either setaceous or laterally flattened; mandibular fan present; maxillae as shown by Parma (1971a:175), Cook (1956:76); anal fan setae plumose, not paired; dorsal process on abdominal segment IX either flat, conical or with short article.

Third Instar Larvae. Most specimens of most species with developing adult eye visible, absent from C. anomalus; antenna with six terminal setae; pair of setae dorso-posterior to antennae simple; 10 post-antennal filaments; prelabral appendages one in front of other, either setaceous or flattened; mandibular fan present; maxillae as shown by Parma (1971a:175); anal fan setae plumose, not paired.

Second Instar Larvae. Some specimens of some species with developing adult eye visible; antenna with six terminal setae; eight postantennal filaments; prelabral appendages lateral to one another, setaceous; mandibular fan present; maxillae as shown by Parma (1971a:175) fan setae plumose, not paired.

First Instar Larvae. Developing adult eye not visible; egg burster on dorsum of head capsule; antenna with four terminal setae; base of

antenna without posterior curve (except C. edulis Edwards; McGowan, 1976:300); two postantennal filaments; prelabral appendages lateral to one another, setaceous; mandibular fan absent; maxillae as shown by Parma (1971a:175); anal fan setae simple, not arranged in pairs.

Eggs. Outline oval; some species with eggs placed in jelly-like matrix; white when laid, later light to dark brown; chorion transparent; at least for species of Chaoborus s. str. egg shell canoe-like in shape (Parma, 1971b:32; pers. obs.) with dorsal longitudinal slit (see also descriptions of Schadonophasma species).

3.2 Diagnosis and Description of the Subgenus Schadonophasma

Schadonophasma Dyar and Shannon 1924:209. Type species Corethra trivittata Loew 1862:186 by monotypy. Cook 1956:28. Edwards 1932:26.

Schadanophasma Saether 1970:12 (misspelling).

Saether (1970:14) incorrectly recognized C. nyblaei as type species.

Especially considering the morphological similarity of known stages of Chaoborus species, Lane's (1951:336) suggestion that Chaoborus subgenera be raised to generic rank does not seem to be justified and at least until the world fauna is better understood, subgeneric status should be retained.

Diagnosis

Adult. Total length 5.2-8.5 mm.; general coloration as given by Cook (1956); wings with several spots (Fig. 3C); following more darkly pigmented than rest of thorax - anterior pronotum, dorsal portion of posterior pronotum (some specimens quite lightly); ventral half of preepisternum, anterior half of anterior anepisternum 2, pleural apophysis, anterior-dorsal edge of anepimeron, meron, center of anepisternum 3, scutellum, postnotum two pairs of vittae on scutum; Rsa present and Cu_{2a} faint or absent; wing veins scaled; legs each with apex of femur, apex and base of tibia, apex of first, second and third tarsomeres and all of fourth and fifth tarsomeres darkly pigmented; pulvilli well developed, at least half as long as claws; ommatidia free dorsal part of eye at least as long as three ommatidia (Saether,

1970: Fig. 9); no parascutellar setae. Male, without lobe or stout setae on inner face of basistyle; penis valve with apical claw. Female. Inner face of tarsomere three of midlegs and hindlegs with row of comb-like setae (Fig. 4A); segment X not covered from dorsal view by tergum IX, neither apically bilobed (Cook, 1956: fig. 15A); seminal capsule ovoid with short slightly curved neck (Cook, 1956: fig. 14J); antenna with 13 flagellar articles.

Pupa. Overall coloration from light to dark brown; females slightly darker than males; mature specimens more darkly pigmented along posterior and anterior margin of each abdominal segment, base of some setae, base of paddles; longitudinal stripes parallel to outer margin of abdominal terga and sterna; median rib darker than lateral ribs of paddle; in some, outer and middle ribs equally pigmented but darker than inner rib; when pharate adult developed (abdominal setae of pharate adult visible) pigmented wings and legs visible, penis valves of males with apical claw (Fig. 3B); WS/LS of both male and female 1.20-1.89; median rib with plumose seta 0.47-0.79 of its length from base and simple seta near apex; shagreening at base of paddles; outer rib of paddle with only sparse shagreening; median rib almost extended to margin of paddle and curved apically (Fig. 2C,D); respiratory horns spindle shaped; length of respiratory horn/width of respiratory horn of male 3.30-4.71, of females 3.23-4.80; chaetotaxy as shown on Figure 6, setae present as shown by Belkin et al. (1970) except seta 4-II present; male genital sac length 932-1298 µm, width 189-307 µm, length/width 3.24-5.05.

Fourth Instar Larva. Total length 11.4-20.3 mm.; head capsule length 1404-2620 µm; seta on anterior face of antenna inconspicuous; AS/AL 0.75-0.93; antenna with curve at posterior base (Fig. 7D); tentorium pigmented, thick, conspicuous (Fig. 2A); dorsal process on abdominal segment IX flat (Fig. 2B; 8C,D); head capsule colorless to dark brown; more pigmented specimens with posterior margin, dorsal surface on head capsule, area around anterior tentorial pit, and line of attachment of mandible conspicuously pigmented; lateral outline of dorsal surface of head capsule as shown by Saether (1970: fig. 11A,B,C) and Figure 2A and 7I; longest mandibular tooth elongate, with curve about 0.75 from base (Fig. 8B; Saether, 1970: fig. 11K; Felt, 1904: Fig. 99); head capsule with microsculpture arranged polygonally on posterior edge (Fig. 4B); additional features in key.

Third Instar Larva. As fourth instar larva except following: total length 7.0-13.0 mm.; head capsule length 944-1440 µm; lateral outline of dorsal surface of head capsule as in Figure 7H; microsculpture on posterior margin of head capsule not obviously polygonal; antenna with curve at posterior base (Fig. 7C); AS/AL 0.53-0.90; longest mandibular tooth elongate, with or without slight curve about 3/4 from base; additional features in key.

Second Instar Larva. As fourth instar larva except following: total length 4.7-7.3 mm.; head capsule length 522-760 µm; lateral outline of dorsal surface of head capsule as in Figure 7G: microsculpture on posterior margin of head capsule not polygonal; antenna with only slight curve at posterior base (Fig. 7B); AS/AL 0.38-0.72; longest

mandibular tooth elongate, without curve; additional features in key.

First Instar Larva. As fourth instar except following: total length 2.0-4.5 mm.; head capsule length 294-494 µm; lateral outline of dorsal surface of head capsule as shown in Figure 7E,F; microsculpture on posterior margin of head capsule not polygonal; antenna without curve at posterior base (Fig. 7A); AS/AL 0.24-0.40; mandible as in Figure 8A; additional features in key.

Description

Description of the subgenus is provided in the description of Chaoborus, the diagnosis of Schadonophasma, and the following keys and descriptions of species.

3.3 Key to the Species of Schadonophasma

Species of Schadonophasma are morphologically very similar and are therefore difficult to identify. No single character can or should be relied upon to identify larvae, pupae or adults to species; thus, to be confident of a correct determination, all characters described should be examined. Because of this overlap of range of variation it is best to identify several individuals from a sample and opposites of the couplet should be compared.

Male adults

The shape of the penis valves is particularly important but difficult to use in identifying males. It is imperative that the penis valves be examined from a number of orientations until their shape approximates those illustrated.

1. Penis valve head elongate with claw mostly parallel to longitudinal axis of penis valve (Fig. 10A-O); penis valve length 145-232 µm; Y/X wing ratio 1.17-3.22; length of tarsomere five of foreleg 186-273 µm; length of claw of foreleg 53-83 µm; coloration of vittae generally black or very dark brown ..... C. trivittatus (Canada, eastern and western U.S.A.)

Penis valve shape not as above (Fig. 11A-N) or if similar (Fig. 11 O,P), specimen from Fennoscandia; penis valve length 191-232 µm; Y/X wing ratio 1.64-3.62; length of tarsomere five of foreleg 220-284 µm; length of claw of foreleg 65-88 µm; coloration of vittae generally brown 2

2. Penis valve head bulbous with claw mostly perpendicular to longitudinal axis of penis valve (Fig. 11 A-O); Y/X wing ratio 1.64-3.62; length of claw of foreleg 65-88 µm
..... C. cooki (Canada)

Penis valve head elongate with claw mostly perpendicular to longitudinal axis of penis valve (Fig. 11 O,P); Y/X wing ratio 1.88-2.13; length of claw of foreleg about 85 µm
..... C. nyblaei (Fennoscandia)

Female adults

Egg number and type, when present in the abdomen and in good condition, are consistent and reliable characters for species determination.

1. Seminal capsules 71-102 µm in diameter; Y/X wing ratio 1.19-3.22; length of tarsomere five of foreleg 232-290 µm; length of claw of foreleg 64-81 µm; prementum length 325-510 µm; coloration of vittae generally black or very dark brown; distance from anterior tip of longest ovary to apex of abdomen 0.71-1.11 times total length of abdomen of teneral females; total number of eggs 150-329 in nulliparous individuals; eggs, if present, of parous individuals with no obviously thick exochorion (Fig. 9A)
..... C. trivittatus (Canada, eastern and western U.S.A.)

Seminal capsules 65-79 µm in diameter; Y/X wing ratio 2.03-5.83; length of tarsomere five of foreleg 232-325 µm; length of claw of foreleg 64-104 µm; prementum length 458-574 µm; coloration of vittae generally brown; distance from anterior tip of longest

ovary to apex of abdomen 0.32-0.62 times total length of abdomen of teneral females (unknown for C. nyblaei); total number of eggs 58-144 in nulliparous individuals; eggs, if present, of parous individuals with obvious thick exochorion (Fig. 9 B,C) ..... C. cooki (Canada)

C. nyblaei (Fennoscandia)

Male and female pupae

Male and female pupae are distinguished from one another by the shape of their genital lobes (Fig. 2C,D), Deonier (1943: fig. 1,2).

Saether's (1972) key to pupae should read 'abdominal segment VII' instead of 'abdominal segment VIII' and couplet 7(4) (pg. 271) should read 'Median rib of anal paddle with a minute seta at apex and a single plumose seta medially (Fig. 12 O-Q); greatest width of thoracic organ at or below the middle'.

Male pupae

1. Width of abdominal segment VII 1074-1794 µm; respiratory horn length 1.18-1.48 mm.; non-teneral live individuals with abdomens nearly vertical (Fig. 5B)..... C. trivittatus (Canada, eastern and western U.S.A.)

   Width of abdominal segment VII 1605-1947 µm; respiratory horn length 1.31-1.64 mm.; non-teneral live individuals with tip of abdomen nearly horizontal (unknown for C. nyblaei) (Fig. 5A) 2

2. WS/LS 1.40-1.69..... C. cooki (Canada)

   WS/LS 1.63-1.74..... C. nyblaei (Fennoscandia)

Female pupae

1. Width of abdominal segment VII 1239-2266 µm; WS/LS 1.25-1.62; mature individuals (pharate adult setae evident) with abdomen full of eggs; non-teneral live individuals with abdomen nearly vertical (Fig. 5B)..... C. trivittatus (Canada, eastern and western U.S.A.)

   Width of abdominal segment VII 1605-2382 µm; WS/LS 1.43-1.89; mature individuals (pharate adult setae evident) with ovaries extended to at most abdominal segment V (unknown for C. nyblaei); non-teneral live individuals with tip of abdomen nearly horizontal (unknown for C. nyblaei) Fig. 5A) 2

2. Width of abdominal segment VII 1605-2230 µm; WS/LS 1.43-1.87 ..... C. cooki (Canada)

   Width of abdominal segment VII 2030-2384 µm; WS/LS 1.71-1.89 ..... C. nyblaei (Fennoscandia)

Larvae

Roman numerals refer to larval instars. C. nyblaei I, II, and III are unknown.

1. Prelabral appendages one in front of other 5

   Prelabral appendages lateral to one another 2

2. Egg burster on dorsum of head capsule (Fig. 7E,F); antennae each with four terminal setae; two postantennal filaments; mandibular fan absent; most anal fan setae arranged in pairs 3

   No egg burster on dorsum of head capsule (Fig. G-I); antennae each with six terminal setae; eight postantennal filaments present; mandibular fan present; no anal fan setae arranged in pairs 4

3. Egg burster on dorsum of head capsule not pigmented, shaped as in Figure 7K; head capsule length 294-368 µm; antennal length 79-115 µm; antennal blade length 176-232 µm ..... C. trivittatus I (Canada, eastern and western U.S.A.)

   Egg burster on dorsum of head capsule pigmented, and shaped as in Figure 7J; head capsule length 347-493 µm; antennal length 103-132 µm; antennal blade length 208-288 µm ..... C. cooki I (Canada)

4. Head capsule length 522-650 µm; LB/AL 1.02-1.16; 8-14 mandibular fan bristles; 16-21 anal fan setae ..... C. trivittatus II (Canada, eastern and western U.S.A.)

   Head capsule length 638-760 µm; LB/AL 0.91-1.07; 7-9 mandibular fan bristles; 19-26 anal fan setae ..... C. cooki II (Canada)

5. Head capsule length 944-1440 µm; antennal length 423-673 µm; postantennal filament length 354-578 µm 6

   Head capsule length 1404-2620 µm; antennal length 623-1235 µm; postantennal filament length 555-1015 µm 7

6. AS/AL 0.58-0.90; PAL/PAW 3.36-15.00; 9-24 mandibular fan bristles; 19-28 anal fan setae..... C. trivittatus III (Canada, eastern and western U.S.A.)

   AS/AL 0.53-0.81; PAL/PAW 3.56-6.60; 8-12 mandibular fan bristles; 22-23 anal fan setae..... C. cooki III (Canada)

7. Head capsule length 1404-2384 µm; antennal length 632-1195 µm; LB/SB 1.47-2.92; PAW/PAW 2.63-9.88; 11-36 mandibular fan bristles; 21-33 anal fan setae..... C. trivittatus IV (Canada, eastern and western U.S.A.)

   Head capsule length 1707-2620 µm; antennal length 789-1235 µm; LB/SB 1.14-2.13; PAL/PAW 2.00-5.30; 8-17 mandibular fan bristles; 28-40 anal fan setae.....8

8. Postantennal filament length 631-944 µm; prelabral appendage length 186-306 µm; PAL/PAW less than 4.16; 28-38 anal fan setae..... C. cooki IV (Canada)

   Postantennal filament length 684-1015 µm; prelabral appendage length 300-348 µm for specimens with undamaged tip (tip not coming to flat end (Fig. 15E-H); PAL/PAW for such specimens 3.58-5.13; 34-40 anal fan setae..... C. nyblaei IV

Eggs

1. Laid in spiral arrangement in flat jelly-like matrix; exochorion thin, without sculpturing (Fig. 9A; 4C); length/width 2.85-3.16 ..... C. trivittatus (Canada, eastern and western U.S.A.)

   Laid in a more or less spherical mass (unknown for C. nyblaei); exochorion thick with hexagonal sculpturing (Fig. 9B,C; 4D); length/width without exochorion 2.36-2.77 (unknown for C. nyblaei)
   ..... C. cooki (Canada)
   ..... C. nyblaei (Fennoscandia)

3.4 Description of Chaoborus trivittatus (Loew)

Corethra trivittata Loew 1862:186. Holotype adult male, labelled:

'Me', 'Loew Coll.', 'Type 4050', 'trivittata'; (MCZ).

Johannsen 1903:398. Not Dyar 1902:201.

Sayomyia trivittata Felt 1904:361. Felt 1905:497.

Sayomyia knabi Dyar 1905:16. Holotype third instar larva, labelled:

'Sayomyia trivittata (trivittata crossed out), Springfield Mass, F. Knab', '96'. A figure of the prelabral appendage on the label is identical to that drawn by Dyar 1905:14; (USNM).

Chaoborus trivittatus Dyar and Shannon 1924:212. Saether 1970:23. Johnannsen 1934:44. Dickinson 1944:351.

Chaoborus trivattus Saether 1970:23 (misspelling).

Chaoborus nyblaei Cook 1956:28 in part (not Zetterstedt). Saether 1970: 14 in part. Matheson 1944:94.

Chaoborus brunskilli Saether 1970:21. Details of holotype and paratype given by Saether (1970). Label of holotype reads 'L. 244' but this is probably incorrect and should read 'L. 241'; (CNC).

Characters tested to distinguish adults of Schadonophasma species are described here to supplement those descriptions by Saether (1970).

Description

Males. General coloration of most specimens dark grayish brown; specific pigmentation as other members of subgenus; penis valves as shown in Figure 10A-O. Measurements and proportions: see Table 2.

Females. Coloration as for males. Measurements and proportions: see Table 3.

Male pupae. Non-teneral live individuals with tip of abdomen in nearly a vertical position when at rest (Fig. 5B); coloration as other members of subgenus. Measurements and proportions: see Table 4.

Female pupae. Non-teneral live individuals with tip of abdomen in nearly vertical position when at rest (Fig. 5B); mature individuals (pharate adult setae evident) with ovaries extended to least abdominal segment III; coloration as other members of subgenus. Measurements and proportions: see Table 5.

Cook (1956:31) reported respiratory horn length of specimens from Green Valley, California to be 1.02-1.13 mm..

Fourth instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 6.

Third instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 7.

Second instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 8.

Table 2. Descriptive statistics for male adult C. trivittatus. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm.)	18	6.4-8.6	7.62	0.90	0.28
No. pronotal setae	24	17-45	30.9	11.2	3.0
No. postpronotal setae	26	3-10	6.3	2.5	0.7
No. supraalar setae	26	22-61	42.2	12.7	3.3
Y/X	156	1.17-3.22	1.810	0.435	0.046
Rsa vein length	21	29-232	120	87	25
P_1 Ta_5	20	186-273	235.2	33.4	10.0
P_2 Ta_5	20	191-255	228.3	26.1	7.8
P_3 Ta_4	17	254-383	334.0	61.6	19.9
P_1 claw length	22	53-83	66.9	12.1	3.4
P_1 pulvilli length	22	26-44	39.4	7.4	2.1
Basistyle length	20	519-732	653	99	30
Dististyle length	24	437-637	558	85	23
HV	17	1.26-1.54	1.375	0.104	0.034
No. setae on tergite IX	110	6-21	12.5	4.8	0.6
Penis valve length	112	145-232	194.4	27.1	3.4

Table 3. Descriptive statistics for female adult C. trivittatus. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm.)	21	5.3-8.9	7.00	1.36	0.40
Length of penultimate article	18	162-191	175.9	16.3	5.1
Length of ultimate article	18	168-261	200.4	33.8	10.6
P/U	18	0.75-1.14	0.894	0.152	0.048
Head width	21	838-1132	1025	118	34
Prementum length	21	325-516	445	68	20
HW/PL	21	1.94-3.23	2.325	0.423	0.123
Length of third palpal article	21	215-307	254	38	11
No. preepisternal setae	21	4-14	9.4	4.2	1.2
No. anepisternal setae	20	14-35	24.0	8.7	2.6
No. upper mesepimeral setae	20	10-40	20.5	11.0	3.2
No. supraalar setae	22	35-72	52.7	17.7	5.0
Y/X	110	1.19-3.22	2.118	0.563	0.072
Claw length of P_1	18	64-87	71.5	9.9	3.1
Pulvilli length of P_1	18	35-58	43.5	8.6	2.7
P_1 Ta_5	19	232-290	248.8	22.1	6.7
P_2 Ta_5	19	186-319	235.7	41.4	12.5
P_3 Ti	20	2077-2844	2375	291	86
P_3 Ta_1	19	1204-1829	1404	251	76
P_3 Ta_5	19	203-297	257.6	32.3	9.8
P_1 L/R	19	0.53-0.66	0.591	0.047	0.014
No. setae in P_2 Ta_3 comb	18	13-27	19.5	6.0	1.9
No. setae in P_3 Ta_3 comb	14	10-22	16.3	5.1	1.8
Seminal capsule diameter	16	71-103	90.6	12.0	4.0

Table 4. Descriptive statistics for male pupae of C. trivittatus. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm.)	60	4.6-6.9	5.99	0.73	0.12
Respiratory horn length (mm.)	44	1.18-1.48	1.330	0.126	0.025
Respiratory horn width (mm.)	43	0.27-0.44	0.352	0.066	0.014
Abdominal segment VII length	65	885-1169	1028	106	17
Abdominal segment VII width	65	1074-1794	1517	272	45
WS/LS	65	1.21-1.89	1.474	0.183	0.030

Table 5. Descriptive statistics for female pupae of C. trivittatus. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm.)	39	5.1-7.6	6.47	0.87	0.18
Respiratory horn length (mm.)	24	1.20-1.77	1.467	0.246	0.067
Respiratory horn width (mm.)	24	0.30-0.51	0.398	0.099	0.027
Abdominal segment VII length	37	897-1510	1158	202	44
Abdominal segment VII width	37	1239-2266	1727	381	84
WS/LS	37	1.25-1.62	1.488	0.128	0.028

Table 6. Descriptive statistics for fourth instar larvae of C. trivittatus. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	474	1404-2384	1881	280	17
Antennal length	493	632-1195	858	144	9
LB/SB	482	1.47-2.92	2.14	0.33	0.02
LB/AL	513	0.50-0.92	0.751	0.090	0.005
AS/AL	491	0.80-0.93	0.886	0.035	0.002
Postantennal filament length	500	555-968	743	108	6
PAL/PAW	490	2.63-9.88	5.22	1.44	0.09
No. mandibular fan bristles	517	11-36	21.8	5.9	0.4
No. anal fan setae	513	21-33	28.0	2.2	0.1

Table 7. Descriptive statistics for third instar larvae of C. trivittatus. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	80	944-1357	1127	140	21
Antennal length	83	423-650	509	91	13
LB/SB	77	1.89-2.70	2.26	0.231	0.035
LB/AL	82	0.73-0.96	0.842	0.065	0.010
AS/AL	83	0.58-0.90	0.770	0.097	0.014
Postantennal filament length	88	354-578	440	79	11
PAL/PAW	88	3.36-15.00	6.72	2.68	0.38
No. mandibular fan bristles	82	9-24	13.6	5.9	0.9
No. anal fan setae	87	19-28	23.8	3.3	0.5

First instar larvae. Egg burster on dorsum of head capsule not as prominent (Fig. 7F) as that of C. cooki first instar larvae; pigmentation of egg tooth and posterior margin of head capsule not nearly as dark as that of C. cooki; coloration of head capsule very light. Measurements and proportions: see Table 9.

Eggs. Laid in spiral arrangement in disc of jelly-like matrix; egg with thin exochorion (Fig. 9A) with no sculpturing (Fig. 4C). Measurements and proportions: see Table 10. Egg shell as in Figure 9D.

Bionomics

Individuals overwinter as fourth instar larvae and are mostly restricted to permanent lentic habitats ranging from small shaded ponds to large deep lakes in woodland. Although some larvae live in temporary waters, they cannot successfully overwinter in these habitats. Adults emerge under spring conditions in Alberta. Records from elsewhere indicate some multivoltine populations (pg. 152).

Deviation of Specific Epithet

'Trivittatus' is derived from Latin (tri - three; vitta - stripe) and refers to the three vittae (actually four but two are very proximate) on the scutum of the adult.

Distribution

Specimens of this species have been collected in woodland areas throughout Canada but are restricted to western United States in California, Oregon, Washington and Montana and to northeastern United States (Fig. 16,17). Lack of records from north central Canada and

Table 8. Descriptive statistics for second instar larvae of C. trivittatus. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	18	522-650	573	44	14
Antennal length	21	215-285	241	21	6
LB/SB	20	1.81-2.38	2.08	0.235	0.070
LB/AL	21	1.02-1.15	1.09	0.058	0.017
AS/AL	20	0.53-0.72	0.605	0.078	0.023
Postantennal filament length	21	203-249	227	20	6
No. mandibular fan bristles	19	8-14	9.9	2.7	0.8
No. anal fan setae	22	16-21	18.9	1.9	0.5

Table 9. Descriptive statistics for first instar larvae of C. trivittatus. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	26	294-368	333	31	8
Antennal length	28	79-115	97.0	11.5	2.9
LB/AL	28	1.85-2.78	2.19	0.26	0.07
AS/AL	27	0.23-0.39	0.301	0.660	0.017
Postantennal filament length	15	73.5-97.0	85.26	11.43	3.87
No. anal fan setae	26	16-23	20.0	2.4	0.6

Table 10. Descriptive statistics for eggs of C. trivittatus. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Length	12	655-684	668	14.3	5.5
Width	12	215-232	224	8.7	3.3
Length/width	12	2.85-3.16	2.99	0.137	0.053

Alaska probably reflect lack of collecting. C. trivittatus is clearly restricted to woodland. Records from southern Alberta (Fig. 17), for example, are clearly the eastern limit of this species in this area. I attempted to collect east of these localities but with no success. In the Rocky Mountains, the species has not been found above treeline. The single record from Baffin Island is suspect. No other records of Schadonophasma are north of treeline. However, for the sake of completeness I have included the record on the distribution map.

Records of C. trivittatus from Wisconsin reported by Dickenson (1944) are undoubtedly correct. Cook's (1956) objection that he found one specimen to be a culicine erroneously assumes only one specimen. However, Dickenson (1944) also recorded larvae which could only be those of C. trivittatus (length of two centimeters). In addition, I have examined specimens from Vilas County, Wisconsin which are C. trivittatus.

Cleugh and Hauser (1971) give the exact localities for the numbered lakes near Kenora, Ontario.

Localities

Male adults

CANADA

ALBERTA: Banff, 24-VII-1918 (1 BMNH, 4 USNM); 10 mi. (16 km.) W. Jasper, 4-VI-1976 (5 CNC, 5 USNM, 8UASM, 20 ABOr); Bigoray River, oxbow lake, 25-V-1971 (1 OASa); 1.5 mi. (2.4 km.) W. Edmonton, 3-V-1976 (5 CNC, 5 USNM, 25 ABOr, 7 UASM); Edmonton, 17-V-1974 (1 ABOr); BRITISH COLUMBIA: Kaslo, 13-21-VI-? (7 USNM); Terrace, 18-VI-1960 (5 CNC, 1 ABOr); Prince Rupert, 13-V-1919 (1 CNC); Atlin,

5-VII-1955 (6 CNC, 1 ABOr); Lower Post, 20-VI-1948 (2 CNC); NORTHWEST TERRITORIES: Aklavik, 28-VIII-1932 (1 USNM); Lake Harbour, Baffin Island, 7-VIII-1935 (1 CNC); NOVA SCOTIA: 4-III-1935 (reared) (1CNC); ONTARIO: North Burgess Twp., 15-20-V-1970, (6 CNC); Black Lk., 44°46'N 76°18'W, 26-IV-1973 (8 CNC, 1 ABOr); Kenora, Lk. 241, 13-VI-1968 (reared) (1 CNC); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-IV-1973 (3 CNC), 5-14-V-1973 (12 CNC, 2 ABOr); YUKON TERRITORY: Whitehorse, 14-21-V-1949 (5 CNC, 1 ABOr).

UNITED STATES

CALIFORNIA: Alameda Co.: Oakland, 4-V-1937 (2 CAS); Humboldt Co.: Mad River Beach, 13-VIII-1948 (7 USNM); Monterey Co.: Pacific Grove, 18-VII-1940 (2 USNM); San Luis Obispo Co.: Oceano Beach, 20-VIII-1948 (1 USNM); Santa Clara Co.: Stanford University, ?-III-1903 (1 CUNY, 2 USNM), 28-V-1903 (1 USNM); MAINE: (1 MCZ); MASSACHUSETTS: Worcester Co.: Worcester, 23-IV-? (2 MCZ); Audorra (specific locality unknown), (1 USNM); NEW HAMPSHIRE: Belknap Co.: Center Harbor, (7 USNM); Rockingham Co.: Hampton, 21-IV-1906 (1 MCZ); NEW YORK: Essex Co.: Elizabethtown 10-13-VI-1904 (1 CUNY, 1 USNM); OREGON: Multnomah, Clackamas and Washington Co.: Portland, (1 USNM); WASHINGTON: Kitsap Co.: Bremerton, 2-V-1924 (1 USNM); Port Madison, 3-II-1934 (reared) (2 USNM); Hoodsport, 3-9-V-1924 (2 BMNH, 6 USNM).

Female adults

CANADA

ALBERTA: 10 mi. (16 km.) W. Jasper, 4-VI-1975 (8 ABOr, 3 CNC); 1.5 (2.4 km.) W. Edmonton, 13-V-1975 (15 ABOr, 8 CNC, 10 UASM); BRITISH COLUMBIA: Kaslo, 13-20-VI-? (7 USNM); Victoria, 4-X-1922 (1 CNC); Canim Lk., 23-VI-1938 (2 CNC); Terrace, 7-18-VI-1960 (8 CNC, 1 ABOr); Atlin, 5-VII-1955 (5 CNC); Lower Post, 20-VI-1948 (1 CNC); NORTHWEST TERRITORIES: Aklavik, 28-VIII-1932 (1 USNM); ONTARIO: Cordova Mines, 7-IX-1962 (2 CNC); North Burgess Twp., 15-20-V-1970 (1 CNC); Black Lk., 44°46'N 76°18'W, 26-IV-1973 (4 CNC); QUEBEC: Old Chelsea, 20-IX-1961 (12 CNC, 1 ABOr); YUKON TERRITORY: Whitehorse, 15-V-1944 (1 CNC), 16-V-1949 (1 CNC), 15-19-V-1950 (1 CNC).

UNITED STATES

CALIFORNIA: Alameda Co.: Berkeley, 5-VI-1948 (1 USNM); Oakland, 4-V-1937 (1 CAS); Humboldt Co.: Mad River Beach, 13-VIII-1948 (7 USNM); Kings Co.: Hanford, 8-VII-1947 (1 USNM); Madero Co.: Matadero Creek, 24-V-1937 (1 CAS); Mariposa Co.: Yosemite, 15-V-1916 (1 USNM); Mendocino Co.: Garcia River, 30-VII-1948 (1 USNM); Placer Co.: NW of Cisco, Nevada Co., 16-V-1948 (1 USNM); Placer and El Dorado Co.: Lake Tahoe, 17-IX-1915 (1 USNM); San Luis Obispo Co.: Oceano Beach, 20-VIII-1948 (2 USNM); Santa Clara Co.: Stanford University, III-1903 (1 CUNY, 6 USNM); MONTANA: Glacier Co.: North Fork Rangers Station, Glacier National Park, 13-V-1926 (1 USNM),

5-VI-1926 (1 USNM); NEW HAMPSHIRE: Belknap Co.: Center Harbor, (2 USNM); Rockingham Co.: Hampton, 19-VI-1906 (1 MCZ); NEW YORK: Essex Co.: Elizabethtown, 10-11-VI-1904 (2 USNM), 25-VIII-1904 (1 CUNY); Rockland Co.: Bear Mnt., 25-IX-1927 (1 USNM); OREGON: Multnomah, Clackamas and Washington Co.: Portland, 4-VII-1934 (2 USNM); WASHINGTON: Kitsap Co.: Manitou Beach, 13-III-1934 (reared) (1 USNM); Port Madison, 3-II-1934 (1 USNM); Mason Co.: Hoodsport, 5-9-V-1924 (4 USNM).

Male pupae

CANADA

ALBERTA: 1.5 mi. (2.4 km.) W. Edmonton, 8-V-1974 (2 ABOr, 1 UASM); BRITISH COLUMBIA: Kaslo (4 USNM); Eunice Lk., 24-V-1971 (3 OASa); Lower Post, 19-20-VI-1948 (20 CNC); NEWFOUNDLAND: 3 mi. (4.8 km.) N. St. John's, 4-VI-1975 (1 ABOr); ONTARIO: Kenora, Lk. 241, 13-VI-1968 (1 CNC); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-21-IV-1973 (12 CNC, 2 ABOr).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (5 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (9 USNM); MICHIGAN: Gogebic Co.: Hummingbird Lk., 15-VIII-1971 (1 OASa); WASHINGTON: Snohomish Co.: Everett, 7-IV-1949 (3 WSUP); Hall Lk., 29-VIII-1952 (11 WSUP).

Female pupae

CANADA

ALBERTA: 53 mi. (85 km.) N. Coleman, 3-VIII-1975 (2 ABOr, 2 UASM); 1.5 mi. (2.4 km.) W. Edmonton, 8-V-1974 (2 ABOr, 2 UASM); BRITISH COLUMBIA: Kaslo (4 USNM); Lower Post, 19-20-VI-1948 (8 CNC); NEWFOUNDLAND: 3 mi. (4.8 km.) N. St. John's, 4-VI-1975 (1 ABOr); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-IV-1973 (1 CNC), 5-6-V-1973 (3 CNC).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (2 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (8 USNM): Snohomish Co.: Hall Lk., 29-VIII-1952 (4 WSUP).

Fourth instar larvae

CANADA

ALBERTA: 2.5 mi. (4.0 km.) NW Edmonton, 13-IX-1970 (4 ABOr); 1.5 mi. (2.4 km.) W. Edmonton, 26-IV-1975 (25 ABOr, 13 CNC, 5 UASM); 2 mi. (3.2 km.) N. Devon, 23-IX-1972 (1 ABOr); 4.7 mi. (7.6 km.) NW Mountain Park, 21-IX-1974 (20 ABOr, 7 CNC, 5 UASM); East Henry Pond, Jasper National Park, 12-IX-1968 (1 FWI, 4 CNC); 1.5 mi. (2.4 km.) S. Robb, 23-VII-1975 (50 ABOr, 6 UASM); 53 mi. (85 km.) N. Coleman,

3-VIII-1975 (10 ABOr, 2UASM); 43 mi. (69 km.) N. Coleman, 3-VIII-1975 (1 ABOr); 33 mi. (53 km.) N. Swan Hills, 1-IX-1975 (12 ABOr); 62 mi. (100 km.) N. Coleman, 3-VIII-1975 (15 ABOr, 7 UASM); 38 mi. (61 km.) N. Swan Hills, 1-IX-1975 (11 ABOr); 14 mi. (22 km.) E. Fox Creek, 30-VIII-1975 (11 UASM); 1 mi. (1.6 km.) N. Swan Hills, 1-IX-1975 (11 ABOr); 23 mi (69 km.) E. Fox Creek, 30-VIII-1975 (11 ABOr); 43 mi. (69 km.) E. High Prairie, 1-IX-1975 (11 ABOr); 3 mi. (4.8 km.) S. Hinton, 23-VII-1975 (11 ABOr); 32.5 mi. (52 km.) N. Banff, 8-IX-1976 (11 ABOr); Pond nr. Kinky Lk., 11-XI-1976 (10 ABOr); 26 mi. (42 km.) N. Sundre, 11-X-1976 (11 ABOr); 47 mi. (76 km.) N. Nordegg, 7-IX-1976 (11 ABOr); 12 mi (19 km.) S. Seebe, 3-VIII-1975 (11 ABOr); 10 mi. (16 km.) W. Jasper, 27-IV-1976 (10 ABOr); 58 mi. (93 km.) S. Seebe, 3-VIII-1975 (11 ABOr); 28 mi. (45 km.) E. Jasper, 27-IV-1976 (11 UASM); 4 mi. (6.4 km.) W. Jasper, 20-V-1975 (9 ABOr); 5 mi. (8.0 km.) S. Jasper, 18-VI-1975 (12 ABOr); *Pond nr. Cameron Lk., 18-IX-1977 (17 ABOr); *Pond nr. Wabamum Lk., 15-X-1977 (1 ABOr); *Opal, 10-X-1977 (6 ABOr); BRITISH COLUMBIA: 3 mi. (4.8 km.) E. Sicamous, 10-VI-1976 (11 ABOr); Prince Rupert, 13-V-1919 (5 USNM); Kaslo, (5 USUM); 4.8 mi. (7.7 km.) N. Clearwater, 12-VI-1976 (11 ABOr); Eunice Lk., fall of 1971 (4 OASa, 10 ABOr); Lower Post, 19-VI-1948 (11 CNC); Gwendoline Lk., ?-VIII-1973 (10 ABOr); NEWFOUNDLAND: 3 mi. (4.8 km.) N. St. John's, 4-VI-1975 (11 ABOr); 0.4 mi. (0.6 km.) W. Logy Bay, 8-VII-1967 (5 USNM); ONTARIO: Kenora, Lk. 241, 14-V-1969 (3 FWI, 8 CNC); Kenora, Lk. 81, 7-V-1969 (1 FWI, 1 CNC); Kenora, Lk. 230, 14-V-1969 (2 FWI, 2 CNC); Kenora, Lk. 240, 14-V-1969 (1 FWI); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 21-IV-1973 (17 CNC); Lk. a la Croix, 26-VI-1971; Randin Lk., 19-VI-1974 (10 ABOr). YUKON TERRITORY:

Klutlane Glacier moraine, VII-1971 (6 EFCo, 3 ABOr);

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (14 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (12 USNM); Santa Clara Co.: Stanford University, ?-11-1945 (3 EFCo, 11 USNM); MAINE: Piscataquis Co.: Milo, 6-I-1906 (1 USNM); MASSACHUSETTS: Hampden Co.: Springfield, ?-VII-1903 (6 USNM); MICHIGAN: Gogebic Co.: Hummingbird Lk., 15-VIII-1971 (3 OASa, 8 JDA1); Ziesnis Bog, 24-VIII-1971 (1 OASa); WASHINGTON: Pacific Co.: 10 mi. (16 km.) S. South Bend, 19-VI-1977 (1 ABOr); Snohomis Co.: Hall Lk., 8-V-1953 (11 WSUP); WISCONSIN: Vilas Co.: Forest Service Bog, 24-VIII-1971 (1 PASa).

Third instar larvae

CANADA

ALBERTA: 62 mi. (100 km.) N. Coleman, 3-VIII-1975 (7 ABOr, 2 UASM); 53 mi. (85 km.) N. Coleman, 3-VIII-1975 (1 ABOr); 1.5 mi. (2.4 km.) S. Robb, 23-VII-1975 (25 ABOr, 5 CNC); 4.7 mi. (7.6 km.) NW Mountain Park, 21-IX-1974 (2 ABOr); BRITISH COLUMBIA: 4.8 mi. (7.7 km.) N. Clearwater, 12-VI-1976 (7 ABOr); ONTARIO: Kenora, Lk. 230, 14-V-1969 (2 FWI); Kenora, Lk. 241, 13-VI-1968 (1 FWI, 8 CNC); YUKON TERRITORY: Klutlane Glacier moraine, VII-1971 (22 EFCo).

UNITED STATES

MASSACHUSETTS: Hampden Co.: Springfield, (1 USNM), ?-VIII-1903 (5 USNM).

Second instar larvae

ALBERTA: 62 mi. (100 km.) N. Coleman, 3-VIII-1975 (6 ABOr, 2 CNC, 2 UASM); East Henry Pond, Jasper National Park, 12-IX-1968 (4 FWI); NEWFOUNDLAND: 3 mi. (4.8 km.) N. St. John's, 4-VI-1975 (1 ABOr); ONTARIO: Kenora, Lk. 230, 14-V-1969 (5 FWI); Kenora, Lk. 240, 14-V-1969 (1 FWI); QUEBEC: Randin Lk., 19-VI-1974 (2 ABOr).

First instar larvae

ALBERTA: 1.5 (2.4 km.) mi. W. Edmonton, 26-VI-1975 (10 ABOr, 4 CNC); 10 mi. (16 km.) W. Jasper, 18-VI-1975 (8 ABOr, 4 UASM); 20 mi. (32 km.) W. Edson, 9-IX-1976 (1 ABOr); East Henry Pond, Jasper National Park, 12-IX-1968 (1 CNC); NEWFOUNDLAND: 3 mi. N. St. John's, 4-VI-1975 (1 ABOr).

Eggs

ALBERTA: 10 mi. (16 km.) W. Jasper, 31-V-1976 (12 ABOr, 2 egg masses CNC, 2 egg masses UASM).

*Material identified but not measured.

Taxonomic Notes

Historically, recognition of specimens of this taxon has presented difficulties. Edwards (1932:26) incorrectly synonymized C. trivittatus and C. nyblaei. C. trivittatus and C. punctipennis were erroneously considered conspecific by Brunetti (1911:229), Dyar (1902: 201), Giles (1902:502) and Theobald (1901b:296; 1905:43). Distributional information and/or the type of habitat in which the larvae were found suggest that Allan (1973; original material examined), Dodson (1970),

Main (1953; original material examined), Maleug and Hasler (1967), Mykle-bust (1966), Stahl (1966) and Teraguchi and Northcote (1966) incorrectly identified specimens of C. trivittatus as C. nyblaei. Some specimens examined by Smith (1960b) were probably larvae of C. trivittatus as indicated by the number of anal fan setae and PAL/PAW. Similarly, data about overwintering larvae studied by James and Smith (1958) indicate that these were individuals of C. trivittatus. I was unable to confirm the identification of some specimens from British Columbia collected by Hearle (1928) as C. trivittatus.

Shape of the penis valve of the type specimen (Fig. 10 O) confirmed the naming of this species.

Examination of the type of Sayomyia knabi showed that the diagnostically (for that geographical region) thick tentorium of the larvae of C. trivittatus was present. All measurements were within the range of the third instar larvae of C. trivittatus. In addition, the pharate fourth instar larva was evident.

All diagnositic features of C. brunskilli (Saether, 1970:21) are within range of variation of C. trivittatus. Penis valves of the holotype, when reoriented (Fig. 10M), were inseparable from those of C. trivittatus. Specimens of C. brunskilli identified by Anderson and Raasveldt (1974) and Hamilton (1971) are therefore C. trivittatus.

The identification of the specimen from Lac Phillipe, Quebec, as C. trivittatus by Saether (1970) could not be confirmed as the penis valves were distorted. I have not included the specimen in this description.

Previous descriptions of pupae are given by Saether (1970) (as C. trivittatus and C. brunskilli), by Cook (1956) (as C. nyblaei)

and by Felt (1904).

The only useful previous descriptions of fourth instar larvae are those by Saether (1970) (as C. trivittatus and C. brunskilli) and Felt (1904). Cook's (1956) description of larvae of C. nyblaei undoubtedly included specimens of both C. trivittatus and C. cooki (see especially description of head capsule length and PAW/PAW).

Saether (1970) gave the only previous descriptions of first, second and third instar larvae of C. trivittatus (as C. brunskilli).

3.5 Description of Chaoborus cooki Saether

Chaoborus cooki Saether 1970:18. Details of holotype, allotype and paratypes given by Saether (1970); (CNC).

Chaoborus nyblaei Cook 1956:28 in part (not Zetterstedt).

Characters tested to distinguish between adults of Schadonophasma species are listed here to supplement those descriptions by Saether (1970).

Males. General coloration of most specimens light grayish brown; specific pigmentation as other members of subgenus; penis valves as shown in Figure 11A-N. Measurements and proportions: see Table 11.

Females. Coloration as for males. Measurements and proportions: see Table 12.

Male pupae. Non-teneral individuals with tip of abdomen nearly horizontal when at rest (Fig. 5A); coloration as other members of subgenus. Measurements and proportions: see Table 13.

Female pupae. Non-teneral individuals with tip of abdomen nearly horizontal when at rest (Fig. 5A); mature individuals (pharate adult setae evident) with ovaries extended at most to abdominal segment V. Measurements and proportions: see Table 14.

Fourth instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 15.

Third instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 16.

Table 11. Descriptive statistics for male C. cooki. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm.)	14	6.8-9.3	7.81	1.39	0.50
No. pronotal setae	15	19-51	29.2	13.4	4.6
No. postpronotal setae	15	3-17	6.6	6.2	2.1
No. supraalar setae	15	32-48	40.4	9.1	3.1
Y/X	89	1.64-3.62	2.47	0.578	0.082
Rsa vein length	15	162-377	256	97	33
P_1 Ta_5	12	220-284	260.5	31.9	12.3
P_2 Ta_5	14	220-284	256.8	31.9	11.4
P_3 Ta_4	13	278-435	375.0	69.3	25.6
P_1 claw length	15	65-88	73.6	10.6	3.6
P_1 pulvilli length	15	41-65	49.0	9.8	3.4
Basistyle length	15	649-838	755	102	35
Dististyle length	15	507-732	616	87	20
HV	14	1.05-1.53	1.293	0.260	0.093
No. setae on tergite IX	59	7-17	11.0	3.1	0.5
Penis valve length	49	191-232	211.8	16.7	3.2

Table 12. Descriptive statistics for female C. cooki. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm.)	17	5.3-8.5	6.54	1.38	0.45
Length of penultimate article	18	168-226	194.3	21.2	6.6
Length of ultimate article	18	168-237	206.5	33.2	10.4
P/U	18	0.83-1.21	0.953	0.147	0.046
Head width	19	944-1274	1061	120	37
Prementum length	19	441-580	504	56	17
HW/PL	19	1.85-2.44	2.110	0.195	0.060
Length of third palpal article	19	191-302	262	38	1
No. preepisternal setae	19	5-13	8.1	3.4	1.0
No. anepisternal setae	19	8-30	18.6	7.0	2.1
No. upper mespimeral setae	18	9-28	16.6	6.8	2.2
No. supraalar setae	19	38-92	52.4	20.3	6.2
Y/X	100	2.03-5.83	3.741	1.098	0.146
Claw length of P_1	17	64-104	75.4	17.7	5.7
Pulvilli length of P_1	17	35-58	42.3	10.5	3.4
P_1 Ta_5	17	232-325	271.9	43.4	14.1
P_2 Ta_5	15	220-319	262.5	47.4	16.2
P_3 Ti	17	2289-3092	2652	299	97
P_3 Ta_1	17	1204-1829	1599	248	80
P_3 Ta_5	15	249-348	282.3	39.3	13.5
P_1 L/R	I6	0.52-0.68	0.599	0.056	0.019
No. setae in P_2 Ta_3 comb	15	8-16	12.0	4.0	1.4
No. setae in P_3 Ta_3 comb	14	5-14	7.7	3.7	1.3
Seminal capsule diameter	18	65-79	69.8	5.9	1.8

Table 13. Descriptive statistics for male pupae of C. cooki. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm.)	11	5.6-7.7	6.67	1.01	0.41
Respiratory horn length (mm.)	11	1.32-1.64	1.546	0.144	0.058
Respiratory horn width (mm.)	11	0.32-0.45	0.39	0.05	0.02
Abdominal segment VII length	11	968-1227	1145	124	50
Abdominal segment VII width	11	1605-1947	1809	180	72
WS/LS	11	1.40-1.69	1.584	0.148	0.059

Table 14. Descriptive statistics for female pupae of C. cooki. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm.)	28	5.3-7.6	6.37	1.05	0.26
Respiratory horn length (mm.)	25	1.37-1.82	1.631	0.149	0.040
Respiratory horn width (mm.)	25	0.34-0.51	0.439	0.072	0.019
Abdominal segment VII length	28	1074-1357	1220	111	28
Abdominal segment VII width	28	1605-2230	2027	223	56
WS/LS	28	1.43-1.87	1.664	0.182	0.046

Table 15. Descriptive statistics for fourth instar larvae of C. cooki. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	210	1707-2620	2150	255	23
Antennal length	210	789-1235	1001	122	11
LB/SB	201	1.14-2.13	1.52	0.22	0.02
LB/AL	201	0.41-0.81	0.628	0.146	0.014
AS/AL	210	0.79-0.93	0.854	0.036	0.003
Postantennal filament length	210	631-944	802	74	7
PAL/PAW	210	2.11-5.18	3.32	0.84	0.08
No. mandibular fan bristles	213	10-17	13.4	1.8	0.2
No. anal fan setae	211	28-38	32.7	2.4	0.2

Table 16. Descriptive statistics for third instar larvae of C. cooki. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	49	1015-1440	1288	158	30
Antennal length	50	464-673	573	75	14
LB/SB	46	1.67-2.30	1.99	0.240	0.047
LB/AL	49	0.64-0.96	0.794	0.146	0.028
AS/AL	50	0.53-0.81	0.692	0.101	0.019
Postantennal filament length	50	413-543	471	43	8
PAL/PAW	46	3.55-6.60	5.14	1.21	0.24
No. mandibular fan bristles	50	8-12	10.3	1.2	0.2
No. anal fan setae	50	22-33	28.6	3.3	0.6

Second instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 17.

First instar larvae. Egg burster on dorsum of head capsule prominent (Fig. 7E) and pigmented; posterior margin of head capsule noticeably pigmented. Measurements and proportions: see Table 18.

Eggs. Laid in spherical mass with slight amount of jelly-like matrix; egg with thick exochorion (Fig. 9C) with polygonal sculpturing (Fig. 40). Measurements and proportions: see Table 19. Egg shell as in Figure 9E.

Bionomics

Overwinters as egg and immatures are restricted to temporary and occasionally permanent ponds in woodland. Larvae may be collected only during summer months (Fig. 25B). Adults generally emerge later in season than do those of C. trivittatus.

Derivation of Specific Epithet

Named after Dr. E.F. Cook.

Distribution

Specimens of C. cooki have been collected only from Canada and Alaska (Fig. 18,19). Collecting in Alberta has shown that the species is restricted to woodland. Paucity of records as compared to C. trivittatus is explained by lack of collecting in the restricted habitat in which the species is found and the presence of larvae only during the summer months.

Table 17. Descriptive statistics for second instar larvae of C. cook. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	35	638-760	712	51	11
Antennal length	33	273-347	309	23	5
LB/SB	28	2.02-2.97	2.49	0.328	0.083
LB/AL	34	0.91-1.07	0.99	0.058	0.013
AS/AL	33	0.42-0.56	0.479	0.053	0.012
Postantennal filament length	34	215-267	241	19	4
No. mandibular fan bristles	34	7-9	7.9	0.8	0.2
No. anal fan setae	35	19-26	22.0	2.4	0.5

Table 18. Descriptive statistics for first instar larvae of C. cooki. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	20	347-494	432	69	20
Antennal length	20	103-132	117.0	13.5	4.0
LB/AL	20	1.88-2.45	2.15	0.23	0.07
AS/AL	20	0.27-0.38	0.333	0.051	0.015
Postantennal filament length	20	79.4-123.5	93.93	15.24	4.54
No. anal fan setae	19	20-26	23.0	2.4	0.7

Table 19. Descriptive statistics for eggs of C. cooki. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Length with exochorion	13	731-853	804	48.2	17.8
Width with exochorion	13	418-458	431	16-1	6.0
Length/width	13	1.70-2.01	1.86	0.126	0.046
Length without exochorion	13	516-563	530	18.0	6.6
Width without exochorion	13	203-220	214	7.5	2.8
Length/width	13	2.37-2.77	2.47	0.153	0.056

Localities

Male adults

ALBERTA: Nr. George Lk., 30-VII-1974 (1 ABOr); 0.9 mi (1.4 km.) W. George Lk., 13-V-1976 (reared) (20 ABOr, 15 CNC, 10 UASM); Edmonton, 1-VII-1974 (1 ABOr); MANITOBA: Gillam, 19-VI-1950 (1 OASa), 29-30-VI-1950 (6 CNC); Churchill, 24-VII-1947 (1 CNC), 19-VII-1951 (1 CNC), VII-VIII-1950 (4 CNC); NORTHWEST TERRITORIES: Yellowknife, 6-VII-1949 (2 CNC), 17-VII-1949 (1 CNC); Reindeer Depot, 13-VII-1949 (2 CNC); ONTARIO: Chisholm, 5-VI-1959 (4 CNC), 19-VI-1959 (1 CNC); QUEBEC Great Whale River, 28-31-VII-1949 (6 CNC); 13-29-VIII-1949 (2 CNC, 1 OASa); YUKON TERRITORY: Whitehorse, 11-24-VII-1950 (7 CNC); Mi. 87 (Km. 140), Dempster Hwy., 27-30-VI-1973 (8 CNC), 8-13-VII-1973 (11 CNC), 16-17-VII-1973 (6 CNC), 4-8-VIII-1973 (4 CNC).

Female adults

ALBERTA: 0.9 mi. (1.4 km.) W. George Lk., 13-V-1976 (reared) (10 ABOr, 5 CNC, 3 UASM); MANITOBA: Churchill, 22-30-VII-1948 (14 CNC), VII-VIII-1950 (10 CNC), 17-VIII-1951 (1 CNC); ONTARIO: Chisholm, 19-VI-1957 (6 CNC), 3-VI-1959 (1 CNC); QUEBEC: Great Whale River, 29-VIII-1949 (1 CNC); Indian House Lake, 17-VII-1954 (1 CNC); YUKON TERRITORY: Whitehorse, 3-VII-1919 (1 CNC), 7-22-VII-1950 (5 CNC), 1-VIII-1950 (1 CNC); Mi. 87 (Km. 140), Dempster Hwy., 8-13-VII-1973 (15 CNC), 16-17-VII-1973 (17 CNC); 4-8-VIII-1973 (17 CNC).

Male pupae

ALBERTA: 33 mi. (53 km.) S. Jasper, 4-VI-1975 (3 ABOr, 3 UASM); 1.5 mi. (2.4 km.) S. Robb, 23-VII-1975 (3 ABOr); NORTHWEST TERRITORIES: Yellowknife, 6-VII-1949 (3 OASa), 14-VII-1949 (1 CNC); YUKON TERRITORY: Mi. 87 (Km. 140), Dempster Hwy., 13-VII-1973 (1 CNC).

Female pupae

ALBERTA: 43 mi. (69 km.) N. Coleman, 3-VIII-1975 (5 ABOr, 5 UASM); 20 mi. (32 km.) W. Edson, 17-VI-1975 (4 ABOr, 2CNC, 2 UASM); BRITISH COLUMBIA: 4.8 mi. (7.7 km.) N. Clearwater, 12-VI-1976 (4 ABOr); YUKON TERRITORY: Mi. 87 (Km. 140), Dempster Hwy., 13-VII-1973 (8 CNC).

Fourth instar larvae

ALBERTA: 43 mi. (69 km.) N. Coleman, 3-VIII-1975 (13 ABOr); 33 mi. (53 km.) S. Jasper, 4-VI-1975, (5 ABOr, 6UASM); 1 mi. (1.6 km.) S. Jasper, 4-VI-1975 (30 ABOr, 15 UASM, 17 CNC); 14.5 mi. (23.3 km.) W. Jasper, 21-V-1975 (8 ABOr); 4 mi. (6.4 km.) W. Jasper, 20-V-1975 (9 ABOr); 20 mi. (32 km.) W. Edson, 5-VI-1975 (15 ABOr, 5 CNC, 4 UASM), 29-V-1976 (3 ABOr); 1.5 mi. (2.4 km.) S. Robb, 23-VII-1975 (2 ABOr); 1.5 mi. (2.4 km.) W. Edmonton, 12-VI-1975 (5 ABOr, 3 UASM); 0.9 mi. (1.4 km.) W. George Lk., 12-V-1975 (5 ABOr, 5 CNC, 3 UASM: BRITISH COLUMBIA: 4.8 mi. (7.7 km.) N. Clearwater, 12-VI-1976 (1 ABOr); MANITOBA: Gillam, 10-VI-1950 (1 CNC); Churchill, 1-11-VII-1943 (1 USNM), 29-VI-1950 (1 CNC); NORTHWEST TERRITORIES: Pond nr. Harris

River, 2-VI-1973 (1 CNC); ONTARIO: Aberfoyle, 14-V-1974 (1 ABOr); YUKON TERRITORY: Dempster Hwy., 23-30-VI-1972 (13 ABOr); Mi. 87 (Km. 140), Dempster Hwy., 13-VII-1973 (11 CNC); Klutlan Glacier moraine, VII-1971 (20 EFCo, 6 ABOr); *Old Crow, 19-VII-1977 (1 ABOr).

UNITED STATES

ALASKA: Mi. 6 (10 km.), McKinley, 14-VI-1954 (1 USNM); Mi. 13.5 (21.7 km.) Cantwell Rd., 17-VI-1954 (1 USNM).

Third instar larvae

ALBERTA: 1.5 mi. (2.4 km.) W. Edmonton, 26-V-1975 (8 ABOr, 4 UASM); 1 mi. (1.6 km.) S. Jasper, 4-VI-1975 (5 ABOr, 5 CNC, 4 UASM); 20 mi. (32 km.) W. Edson, 29-V-1976 (3 ABOr, 2 CNC, 2 UASM); 0.9 mi (1.4 km.) W. George Lk., 12-V-1975 (8 ABOr, 3 UASM); NORTHWEST TERRITORIES: Pond nr. Harris River, 2-VI-1973 (1 CNC); YUKON TERRITORY: Klutlan Glacier moraine, VII-1971 (6 EFCo).

Second instar larvae

ALBERTA: 1 mi. (1.6 km.) S. Jasper 25-IV-1976 (3 ABOr); 7 mi. (11 km.) E. Obed, 27-IV-1976 (8 ABOr, 4 UASM); 20 mi. (32 km.) W. Edson, 27-IV-1976 (4 ABOr, 4 UASM); 0.9 mi. (1.4 km.) W. George Lk., 24-IV-1976 (8 ABOr, 4 UASM).

First instar larvae

ALBERTA: 1 mi. (1.6 km.) S. Jasper, 25-IV-1976 (8 ABOr, 4 UASM); 20 mi. (32 km.) W. Edson, 27-IV-1976 (4 ABOr, 4 CNC).

Eggs

From male and female adults collected as fourth instar larvae 0.9 mi. (1.4 km.) W. George Lk., Alberta and reared and mated in lab.

*Material identified but not measured.

Taxonomic Notes

Because many specimens of C. cooki key out to C. nyblaei using Saether's (1972) keys, records of C. nyblaei by Anderson and Raasveldt (1974) probably refer to specimens of C. cooki. The numbers of anal fan setae and PAL/PAW recorded by Smith (1960b) suggests that C. cooki larvae were examined. The suggestion by James and Smith (1958) that some of the C. nyblaei population overwinters in the egg stage at Churchill, Manitoba, indicates the presence of C. cooki.

The only previous description of C. cooki is that of the adults, pupae and fourth instar larvae by Saether (1970). Cook (1956) undoubtedly included specimens of C. cooki in his description of C. nyblaei. The larval head capsule length recorded by Cook (1956) as 2.78 mm., larger than any recorded here, probably refers to a specimen of C. cooki. Contrary to Saether's (1970:26) statement, Cook's (1956) description of the abdomen probably included C. cooki.

Saether (1970:20) incorrectly states that C. cooki larvae do not have a dorsal process on abdominal segment IX (see pg. 84).

3.6 Description of Chaoborus nyblaei (Zetterstedt)

Erioptera nyblaei Zetterstedt 1838:830. Three syntypes, all females;

lectotype here designated, labelled: 'Corethr. nyblaei, Z.♀, Erioptera, (illegible word), Lapp Dovre'; one syntype with no label and the other labelled 'Corethr. nyblaei, Z. ♂, Erioptera, (illegible word) Lapp Dovre.'; (ZMLS).

Corethra nyblaei Zetterstedt 1851:3794. Giles 1902:502. Theobald 1901b:291.

Chaoborus nyblaei Edwards 1930:533. Edwards 1932:26. Hirvenoja 1961.

Saether 1970:14 in part.

?Corethra pilipes Gimmerthal 1845:297. Location of male type unknown.

Collected at Riga, Latvijskaja S.S.R.

Male. (n=two, unless otherwise given in parentheses)

Total length 7.9-8.5 mm.; general body coloration light grayish brown; specific pigmentation as other members of subgenus.

Antennae: pedicel width 302-319; length of flagellar articles 1,2-11,12,13: 244-267 µm, 148-151 µm, 354-371 µm, 261 µm; P/U 1.42-.156.

Head: width 1096-1125 µm; width between eyes 313-389 µm; clypeus length 447-464 µm; prementum length 470-493 µm; head width/width between eyes 2.90-3.50; head width/clypeus length 2.42-2.45;

head width/prementum length 2.22-2.40; number of setae on vertex 106 (1); lengths of palp articles one to four: 121-139 µm, 249-261 µm, 244-313 µm, 528 µm (1).

Thorax: number of setae: pronotal 24; postpronotal three to four; proepisternal seven to eight; preepisternal four to seven; anepisternals 12-13; upper mesepimerals 14-15; scutellar 72-88; supraalar 37-38.

Wing: length 4.53-4.63; width 1.03; length/width 4.41-4.51; wing length/head width 4.03-4.15; wing length/length of femur of foreleg 1.68 (1); Y/X 1.88-2.13; Y/Z 1.35 -1.59; Y/R_3 0.75-0.77; Z/M_1 0.44-0.56; R_3/M_1 0.94-0.99; number of setae on squama 38 (1); length of Rsa 271 µm (1).

Haltere: capitulum nearly spherical; two to three anterior setae; two to three posterior setae.

Legs: Foreleg: Fe 2690 µm (1); Ti 1251 µm (1); Ta_1 590 µm (1); Ta_5 249 µm (1); Hindleg: Fe 2997 µm (1). Length of claw of foreleg 85 µm (1); pullvilli length 53 µm (1).

Genitalia: number of setae on tergite IX 10 (1); penis valve length 194-226 µm; penis valve as shown in Figure 11,O and P; basistyle length 702 µm (1); dististyle length 609-632 µm; HR 1.15 (1); HV 1.25-1.39.

Female. (n=three, unless otherwise given in parentheses)

Total length 8.0 mm. (1); general body coloration light grayish brown; specific pigmentation as other members of subgenus.

Antennae: (n=2) pedicel width 162 µm; length of flagellar articles 1,2-11, 12,13: 192-203 µm, 124-138 µm, 180-191 µm, 1972-215 µm; P/U 0.89-0.91.

Head: (n=2) head width 1102 µm; width between eyes 360-400 µm; clypeus length 464-487 µm; prementum length 493-528 µm; head width/width between eyes 2.75-3.06; head width/clypeus length 2.26-2.38; head width/prementum length 2.09-2.24; number of setae on vertex 134-146; length of palp articles one to four: 151-157 µm, 290-313 µm, 302-331 µm, 586-621 µm.

Thorax: Coloration as in male.

Number of setae: pronotals 24-43; 70.0; postpronotals 3-11, 6.7; proepisternal 8-11, 9.3; preepisternal 8-10, 9.0; anepisternals 13-34, 24.0; upper mesepimerals 17-24, 19.3; scutellar 87-119, 98.3; supraalar 53-66, 59.7.

Wing: (n=six, unless otherwise stated) coloration as other member of subgenus. Length 5.5-5.9, 5.9 mm.; width 1.4-1.8, 1.6 mm.; length/width 3.55-4.09, 3.84; wing length/head width 5.17-5.25 (2); wing length/length of femur of foreleg 2.22-2.67 (2); Y/X 2.29-3.43, 3.10; Y/Z 1.33 1.67, 1.53; Y/R_3 0.70-0.93, 0.79; Z/M_1 0.42-0.56, 0.50; R_3/M_1 0.91-1.01, 0.96; Rsa 126-302, 238 µm.

Halteres: capitulum nearly spherical; two anterior setae (2); two to eight posterior setae (2).

Legs: (n=2), coloration as other members of the subgenus.

Foreleg: Fe 2608-2631 µm; Ti 2761-2796 µm; Ta_1 1345-1369 µm; Ta_2 802 µm; Ta_3 625-637 µm; Ta_4 389-401 µm; Ta_5 296-302 µm; Ta_1/Ti 0.49.

Midleg: Fe 2395-2537 µm; Ti 2230-2384 µm; Ta_1 1121-1145 µm; Ta_2 637 µm; Ta_3 496 µm; Ta_4 318-342 µm; Ta_5 273-296 µm; Ta_1/Ti 0.47-0.51.

Hindleg: Fe 2974-3221 µm; Ti 2620-2950 µm; Ta_1 1758-1782 µm; Ta_2 909-944 µm; Ta_3 625-649 µm; Ta_4 366-413 µm; Ta_5 319-325 µm; Ta_1/Ti 0.60-0.67.

Length of claw on foreleg 94 µm; pulvilli length 56-61 µm.

Genitalia: seminal capsule diameter 65-76 µm; 71.4 (4); cerci length 267-284, 274 µm (4).

Male pupa. Measurements and proportions: see Table 20

Female pupa. Measurements and proportions: see Table 21.

Fourth instar larva. Measurements and proportions: see Table 22.

Egg: only eggs dissected from abdomens of females were examined. Measurements are probably not therefore, very accurate. Eggs with thick exochorionic layer (Fig. 9B). Sculpturing of exochorian not discernable. Measurements and proportions: see Table 23.

Bionomics

Probably overwinters in the egg stage. Larvae have been collected from both permanent and possibly temporary lentic habitats (Hirvenoja, 1961). This species may be able to invade temporary ponds. Adults emerge about the end of July.

Derivation of Specific Epithet

Named after Olavus Nyblaeus.

Table 20. Descriptive statistics for male pupae of C. nyblaei. Measurements in µm unless otherwise given.

Character	N	Range	Mean
Total abdomen length (mm.)	4	5.5-5.9	5.7
Respiratory horn length (mm.)	4	1.31.-1.42	1.38
Respiratory horn width (mm.)	4	0.30-0.38	0.33
Abdominal segment VII length	4	1003-1109	1056
Abdominal segment VII width	4	1735-1923	1808
WS/LS	4	1.63-1.74	1.71

Table 21. Descriptive statistics for female pupae of C. nyblaei. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm.)	11	6.4-7.8	7.1	0.74	0.31
Respiratory horn length (mm.)	6	1.59-1.73	1.64		
Respiratory horn width (mm.)	6	0.37-0.46	0.43		
Abdominal segment VII length	11	1144-1310	1223	77	31
Abdominal segment VII width	11	2030-2383	3315	167	67
WS/LS	11	1.71-1.89	1.81	0.082	0.033

Table 22. Descriptive statistics for fourth instar larvae of C. nyblaei. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	25	1853-2596	2231	306	.82
Antennal length	26	870-1160	1037	138	36
LB/SB	26	1.24-1.93	1.54	0.206	0.056
LB/AL	26	0.47-0.74	0.650	0.087	0.023
AS/AL	26	0.78-0.91	0.864	0.044	0.012
Postantennal filament length	26	684-1015	845	122	32
PAL/PAW	25	2.00-5.30	3.56	1.142	0.305
No. mandibular fan bristles	25	8-13	12.3	0.95	0.25
No. anal fan setae	24	34-40	36.6	2.90	0.80

Table 23. Descriptive statistics for eggs of C. nyblaei. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Length without exochorion	14	625-778	670	64	23
Width without exochorion	14	236-330	291	42	15
Thickness of exochorion	6	71-106	88		

Distribution

The distribution of C. nyblaei is shown in Figure 20. Although this species is known from certain records only from Fennoscandia, it may, especially if C. pilipes from Riga, Latvijskaja S.S.R. is conspecific with C. nyblaei, be more widely distributed in the boreal region of the Palaearctic region. If this species has similar requirements as C. trivittatus and C. cooki, C. nyblaei is restricted to areas of boreal woodland.

Localities

Male adults

FINLAND: 2-3 km. SW Nuorgam, 24-VII-1960 (1 ZMHF); SWEDEN: Abisko, 1931 (1 BMNH).

Female adults

FINLAND: 2-3 km. SW Nuorgam, 24-VII-1960 (2 ZMHF); SWEDEN: Abisko, 1931 (1 BMNH); NORWAY: Dovre, 30-VII-? (2 ZMLS); unlabelled specimen from type series (1 ZMLS).

Male pupae

FINLAND: 2-3 km. SW Nuorgam, 24-25-VII-1960 (2 OASa; 2 ZMHF).

Female pupae

FINLAND: 2-3 km. SW Nuorgam, 24-25-VII-1960 (4 OASa; 3 CNC; 4 ZMHF).

Fourth instar larvae

FINLAND: 2-3 km. SW Nuorgam, 24-25-VII-1960 (2 OASa; 2 CNC; 20 ZMHF: 2 ABOr)

Eggs

From females collected as follows: SWEDEN: Abisko, 1931 (1 BMNH); NORWAY: Dovre, 30-VII-? (1 ZMLS).

Taxonomic Notes

Considerable confusion has surrounded the name of this species. Edwards (1920:265), Martini (1931:58), and Séguy (1924:169) incorrectly considered C. nyblaei to be conspecific with C. pallidus (Fabricius). Many authors treated Schadonophasma as monotypic or have followed Saether's (1970) conclusion that C. nyblaei occurs in North America and consequently have incorrectly applied this name to North American specimens of Schadonophasma (Allan, 1973; Anderson and Raasveldt, 1974; Cook, 1956; Dodson, 1970; James and Smith, 1958; James et al., 1969; Jenkins and Knight, 1950; Matheson, 1944; McCloy 1950; Myklebust, 1966; Peus, 1967; Smith, 1960 b; Stahl, 1966).

The only previous detailed description of male adult C. nyblaei, by Saether (1970), was based on a specimen of C. trivittatus from Baffin Island, Canada and the hypopygium of a specimen of C. nyblaei from 2-3 km. SW Nuorgam, Finland. The main diagnostic character was shape of the penis valve. Reorientation of the genitalia of these specimens, however, showed that the characterization by Saether (1970) was incorrect. Penis valves of the specimen from Baffin Island are

typical of C. trivittatus. Those from the specimen from Finland are similar to but different from penis valves of C. trivittatus. I was able to associate the hypopygium from Finland with the rest of the specimen and the description includes this male.

Adult characters described by Saether (1970) but not given here were those which could not be measured.

Pupae and fourth instar larvae have been previously described by Hirvenoja (1961) and Saether (1970).

Of the three syntypes of C. nyblaei only measurements of the female genitalia of the lectotype are included in this description and otherwise the lectotype and the paralectotypes were used only to describe color and wing characters. The features of the adult female prepared from a pupa described by Saether (1970) are not included in this description.

Saether (1970:16) incorrectly states that fourth instar larvae of C. nyblaei do not have a noticable dorsal process on abdominal segment IX (see pg. 84).

The first, second, and third instar larvae of C. nyblaei are unknown.

4. Analysis of Morphological Variation

The following is a discussion of morphological variation of the stages of Schadonophasma species. These results describe differences of eggs, all larval stages, pupae and adults between species. Interpretation of some intraspecific morphological variation as the result of age-related, sex-associated and geographical variation and, as described for C. trivittatus, the result of past distributions is also provided. Detailed study of structure, especially when combined with bionomic and behavioral observations, call allow interpretation of the functional significance of characters. These data thereby provide an enhanced means of understanding intraspecific variation and phyletic relationships. Comparison of results with studies of other Chaoborus species is provided to facilitate further comparison between species of Chaoborus, to reinterpret some past results, and to suggest, in some instances, more likely interpretation of data presented here.

4.1 Artifical Variation

An important source of error in determining intraspecific and interspecific variation of species can result from methods employed in the preservation and/or preparation of specimens. This factor accounts for some variation previously described.

Cook (1956:29) noted that thoracic coloration of adult males of Schadonophasma was related to age of pinned specimens. Ground color

had changed from light grey to yellowish-brown in specimens which had been pinned for more than twenty years. I have not been able to confirm this observation which may be due, in part, to Cook's (1956) inclusion in his analysis of adults of both C. trivittatus and C. cooki which do differ in thoracic coloration. In addition, glue had seeped into the thorax of some of the older pinned specimens producing a darker hue.

The color of all material of any stage appeared to bleach when preserved in ethanol for more than about four or five years. In addition, clearing with KOH also bleaches the color of specimens. It is uncertain, therefore, whether Saether (1967) adequately described the color variation of KOH-treated larvae of C. flavicans.

Saether (1970:21) recognized the distinct conical dorsal process of C. brunskilli (= C. trivittatus) fourth instar larvae as diagnostic. Of all material examined, however, only fourth instar larvae preserved in formalin possessed dorsal processes similar to those of C. brunskilli drawn by Saether (1970: fig. 11Q,R) and ethanol-preserved material exhibited flatter dorsal processes (Fig. 2B; 8C,D). Paratype larvae of C. brunskilli came from two localities. Hamilton (1971) states that the specimens from near Kenora, Ontario were preserved in formalin. Anderson and Raasveldt (1974) do not mention the preservative used to kill the specimens from East Henry Pond, Jasper National Park, Alberta. Main (1953:21) reported reduction in total length of 3.3-11.3% of 23 larvae of C. trivittatus or C. flavicans preserved for 24 hours in formalin. The pronounced dorsal process diagnostic of C. brunskilli is therefore probably a result of shrinkage in formalin.

Saether (1970) erroneously suggested that C. cooki and C. nyblaei

fourth instar larvae do not exhibit pronounced dorsal processes. These observations were caused by coverslips compressing cleared specimens and distorting the abdomens. All uncleared fourth instar larvae of C. cooki subsequently examined had a developed dorsal process (Fig. 8D). Additional specimens of C. nyblaei, which had been cleared but preserved in fluid, were available and I mounted these under coverslips supported by glass chips. The abdomens retained their natural dimensions and this allowed observation of the developed dorsal process (Fig. 8C) similar to those of other fourth instar larvae of Schadonophasma.

McGowan (1976) reported six or eight postantennal filaments for second instar and eight or ten postantennal filaments for third instar larvae of C. edulis. However, C. pallidipes (Theobald), which is presently indistinguishable from C. edulis (compare Green and Young, 1976; McGowan, 1976) has the two posterior postantennal filaments distinctly separated (more so than described for C. flavicans by Balvay (1977c)) from the rest of the filaments and if C. edulis also possess this trait, McGowan's (1976) results reflect the breaking off of this separate pair and the variation is probably an artifact of preparation.

Saether's (1970) misinterpretation of interspecific variation of penis valve shape of adult males because of lack of standard orientation of these is described elsewhere (pg. 133).

4.2 Characters Varying Between Larval Instars

Hennig (1966a) has discussed the importance of making comparisons only between comparable semaphoronts in systematic work. The only difficulty recognizing semaphoronts of Schadonophasma concerns the four larval instars and this section therefore describes differences allowing recognition of each of these.

Data concerning instar differences also allowed comparison of developmental patterns from instar to instar between species and, for some characters, provided important clues for determining the polarity of morphoclines for phyletic studies.

Differences between instars of Chaoborus have been described by Balvay (1977a, 1977b, 1977c), Deonier (1943), Fedorenko and Swift (1972), Green (1972), MacDonald (1956), Maleug (1966), McGowan (1972, 1976), Parma (1969, 1971a), Prokesova (1959), Saether (1967, 1970), Sikorowa (1967b, 1970, 1973), Smith (1960a), Teraguchi and Northcote (1966), von Frankenberg (1915), and Weismann (1866). Few workers have considered geographical variation in their analysis of instar differences (Balvay, 1977a, 1977b, 1977c; Green 1972; Saether, 1967, 1970:22; Sikorowa, 1973).

Sikorowa (1973) showed that C. flavicans larvae collected from ponds or lakes differed significantly in a number of characteristics, suggesting that ecological factors produce at least some variation. One character, the length of the longest antennal blade, differed significantly between first instar larvae collected from these two habitat types implying genetic differences.

It is not known, therefore, what characters can be used with certainty to distinguish instars of material collected over an extensive geographical area and an extensive range of habitats. This analysis provides that information for larvae of C. trivittatus and C. cooki. Although some mistaken interpretations of characters are discussed here, qualitative differences between instars are given in the description of Chaoborus and are not repeated here.

Mensural characters previously found to differ between instars, but not necessarily without some overlap of variation, were total length, distance between anterior and posterior air sacs, head capsule length, antennal length, distance of antennal seta from base of antenna, long antennal blade length, short antennal blade length, AS/AL, LB/SB, postantennal filament length, PAL/PAW, number of mandibular fan bristles, and number of anal fan setae. Total length and distance between anterior and posterior air sacs were not measured because they are clearly related to growth and exhibit continuous variation (Balvay, 1977b; Eggleton, 1932; Fedorenko and Swift, 1972; Hongve, 1975; LaRow and Marzolf, 1970; Lewis, 1975; MacDonald, 1956; Main, 1953; Malueg, 1966; McGowan, 1972; Parma, 1971b; Saether, 1967; Sikorowa, 1973; Smith, 1960a; Teraguchi and Northcote, 1966).

Smith's (1960a) report that C. crystallinus first instar larvae have six terminal antennal setae is probably erroneous. Sikorowa (1973: fig. 13) shows only four setae. Further differences between first instar C. flavicans as described by Parma (1971a) and first instar C. crystallinus as described by Smith (1960a), suggest that some second instar larvae contaminated Smith's (1960a) sample of first instar larvae.

4.2.1 Homologous Structures Between First and Later Larval Instars of Schadonophasma

To accurately depict differences between larval instars, homologous structures should be compared. Failure to do so has led to nomenclatural misinterpretation of certain structures in the past.

There has been confusion concerning the setae of the mandible of first instar larvae of Chaoborus. Parma (1971a:178) suggests that C. flavicans first instar larvae exhibit a mandibular fan composed of three setae but Sikorowa (1967b:88) mentions the presence of four setae. C. astictopus first instars do not have a mandibular fan (Deonier, 1943:385). Saether (1970:22) states that C. brunskilli (= C. trivittatus) first instar larvae have a mandibular fan of nine bristles. Reexamination of the specimen showed a mandible typical of first instars (Fig. 8A) and suggests that the mandibular fan bristles counted were those of the pharate second instar which was present.

All first instar material examined exhibited mandibles similar to that in Figure 8A (also Balvay, 1977c: fig. 4; Weismann, 1866: fig. 22A).

The homologies of structures of the mandible of Chaoborus larvae as considered by all authors are summarized in Table 24.

Balvay (1977c) discusses at length the nomenclature of the mandible of different instars of C. flavicans and gives new names for all structures except the mandibular fan. He showed that the mandibles of second, third and fourth instar larvae were structurally similar to each other but were all different from first instar larval mandibles. Balvay (1977c) considered the "mandibular fan" of first instar larvae to be composed of three setae and to be homologous to the mandibular fan of later instars but does not give any justification

for doing so. A fourth articulated seta between the teeth of the mandible and the "mandibular fan" was considered homologous to one of the mandibular setae (= mandibular spur of Knight, 1971b) of later instars. Mandibular setae of the second instar developed at the base of the mandibular seta of the first instar larval mandible. In addition, a nerve extends from the mandibular seta base in the first instar to the bases of the two mandibular setae of the second instar. The mandibular seta of the first instar larval mandible identified by Balvay (1977c) is therefore clearly homologous to one of the mandibular setae of later instars.

Although Balvay (1977c) mentions that the mandibular setae of the pharate second instar larva cannot develop inside the first instar mandibular seta because of the basal articulation, the tips of the mandibular fan bristles of pharate second instar larvae of both C. trivittatus and C. cooki do develop inside this mandibular seta.

Mandibles of first instar larvae of Chaoborus are similar to those of Mochlonyx (James, 1957: fig. 9) which possess four (only three shown by James) setae, three of which are toothed and are very similar and probably homologous to those of later instars of Mochlonyx (Cook, 1956: fig. 22E; Johannsen, 1934: fig. 155; Meinert, 1886: fig. 65). However, mandibles of second, third and fourth instar larvae of Mochlonyx also bear mandibular fans undoubtedly homologous to the mandibular fans of Chaoborus. The three setae on the mandible of first instar Chaoborus larvae are therefore not homologous with the mandibular fan of later instars as suggested by Balvay (1977c), Parma (1971a), Sikorowa (1967b, 1973), and Smith (1960a), and are mandibular spurs (Knight, 1971b). Only two of the mandibular spurs,

each with a similar pointed mandibular projection at their base, as all four setae of first instars, are retained by later instars. I am not certain the naming of the mandibular fan as the mandibular brush and comb by Knight (1971b) is justified and am therefore retaining the traditional name.

One of two additional setae on the mandible of first instar Chaoborus larvae (Fig. 8A), called spines E_1 and E_2 by Balvay (1977c), is probably homologous with seta O-MP (Knight, 1971b) of some culicid larvae. Both setae are retained in later instars of Chaoborus (Fig. 8B; Balvay, 1977c: fig. 5,6,7). The setae are undoubtedly homologous to the two setae on the mandible of first instar Mochlonyx (James, 1957: fig. 9) and Eucorethra underwoodi Underwood (pers. obs.) larvae. Although lost in later instars of Mochlonyx, these two setae are retained in later instars of Eucorethra underwoodi where they are labelled as the pectinate brush by Knight (1971b: fig. 1d). However, their placement and similarity to those of the mandible of Chagasia bathana (Culicidae) (Knight, 1971b: fig. 2f), suggests one of these is seta O-MP. I therefore label the large seta on the mandible of later instars of Chaoborus as such, although it is not certain which of the two is actually seta O-MP. Knight (1971b) does not label the second seta. Knight (1971b: fig. 1e,f) incorrectly labelled seta O-MP as one of the mandibular spurs on the mandible of C. americanus (incorrectly identified as C. flavicans).

Sikorowa (1967b: fig. 1a,b) erroneously shows both second and fourth instar larvae of C. flavicans with three mandibular spurs.

Previous authors have misinterpreted changes in the anal fan between first and second instar larvae. Balvay (1977b) considered, without justification, each pair of anal fan setae of first instar larvae to correspond to a single anal fan seta of the second instar. Sikorowa (1970) mentions that these pairs of setae arise from a common base. This is not so in any of the material I have examined but the sockets for the two setae are placed laterally very close to one another. This paired arrangement of setae is reflected in all later instars in which, although the setae are in an anterior-posterior plane (Fig. 2B), all anal fan setae are placed alternately slightly one side or the other of the sagittal plan. This and that the number of anal fan setae for first and second instar larvae is nearly identical for both C. trivittatus and C. cooki supports the view that each seta in the first instar corresponds to a single seta in the second instar.

4.2.2 Head Capsule Length

Variation in this measurement is useful to distinguish Chaoborus larval instars (Fedorenko and Swift, 1972; Goldspink and Scott, 1971; LaRow and Marzolf, 1970; Malueg, 1966; MacDonald, 1956; Parma, 1969, 1971a; Prokesova, 1959; Saether, 1967, 1970; Sikorowa, 1973; Teraguchi and Northcote, 1966; von Frankenberg, 1915). However, Balvay (1977c) found that the range of head capsule length overlapped between third and fourth instar larvae of C. flavicans. Variation in lengths of larval head capsules of C. trivittatus and C. cooki (Fig. 21A) shows, consistent with most previous work, no overlap of

Table 24. Comparison of studies of homologies of mandibular structure of larvae of Chaoborus.

First Instar Larvae			Later Instar Larvae		All Instars
Balvay, 1977c	Parma, 1971[a]	Sikorowa, 1967b	Knight, 1971b	Balvay, 1977c	This study
Mandibular fan	Mandibular fan	Mandibular fan	Mandibular spurs	Mandibular setae	Mandibular spurs
Mandibular seta	Mandibular tooth				
Spines E_1, E_2	(not reported)	(not reported)	Mandibular spur	Spines E_1, E_2	Seta O-MP, unnamed seta
			Mandibular comb and brush	Mandibular fan	Mandibular fan

range between any of the instars within each species although ranges of third and fourth instar C. trivittatus are proximate. Head capsule length is sex-associated in fourth instar larvae and therefore probably in third instars and any overlap between these instars, as shown by Balvay (1977b), is probably due to a mixture of male fourth instar and female third instar larvae.

4.2.3 Antennal Length

Antennal length is useful to discriminate all instars (or at least 99% of all specimens when authors do not give ranges) collected at a single locality or in a limited geographical region (Green, 1972; McGowan, 1972, 1974, 1976; Parma, 1971a; Saether, 1970; Sikorowa, 1973). Saether (1967) reported a slight overlap between third (330-420 µm) and fourth (420-640 µm) instar antennal lengths of C. flavicans samples from throughout this species' range. Balvay (1977b) reported overlap of antennal lengths only between second and third instars of this species collected in France. Range of variation for C. trivittatus and C. cooki (Fig. 21B) shows that this character can be used to discriminate all instars. Like head capsule length, to which this character is correlated at least in male larvae, antennal length of third and fourth instar C. trivittatus larvae overlap slightly. As this character also exhibits sex-associated variation in fourth instar larvae, the proximity between antennal lengths of third and fourth instar larvae is probably due in part to this source of variation. This, however, could not fully explain Balvay's (1977b) finding of overlap between only second and third instars.

4.2.4 Distance of Antennal Seta From Base of Antenna/Antennal Length (AS/AL)

Parma (1971a:177), for C. flavicans and Saether (1970:22) for C. brunskilli (= C. trivittatus) showed that differences in AS/AL distinguished all instars, although Balvay (1977b) showed overlap for each instar of C. flavicans. C. trivittatus and C. cooki overlap between second and third and between third and fourth instars (Fig. 22A). Later instars of C. trivittatus exhibit, particularly between second and third instars, a substantial degree of overlap of range of AS/AL. Therefore this character is useful to distinguish all first instar larvae and only some second, third and fourth instar larvae of C. trivittatus and C. cooki. Change in the ratio from instar to instar is more constant in C. cooki than C. trivittatus where there is a more pronounced increase from first to second and a lesser increase from second to third and third to fourth instars.

4.2.5 Length of Long Antennal Blade/Antennal Length (LB/AL)

This ratio distinguishes all first instar larvae of C. cooki and all first and second instars of C. trivittatus from all later instars (Fig. 22B). The character can also be used to distinguish some fourth from third instar larvae of C. trivittatus and some second, third and fourth instar larvae of C. cooki.

4.2.6 Length of Long Antennal Blade/Length of Short Antennal Blade (LB/SB)

First instar larvae do not possess the short antennal blades of later instars. Inequality of length of antennal blades noted by

Balvay (1977b) and Parma (1971a:176) for first instar larvae of C. flavicans is also present in later instars where one of the long antennal blades is slightly shorter than the other three. Both Balvay (1977b) and Parma (1971a:177) have shown that although there were statistical differences between LB/SB of second, third and fourth instars of C. flavicans, there was a good deal of overlap of range. Saether (1967: Table 1) showed overlap of variation of this ratio between third (0.43-0.64) and fourth (0.50-0.60) instar larvae of C. flavicans.

Considerable overlap is exhibited between second, third and fourth instars of C. brunskilli (= C. trivittatus) (Saether, 1970:22). LB/SB overlaps in range between the last three instars of both C. trivittatus and C. cooki (Fig. 23A). There were differences in the pattern of change of LB/SB from instar to instar between C. trivittatus and C. cooki. At least some individuals of C. cooki can be identified to instar using this character where the ratio decreases with each successive instar. The range of ratio for the three later instars of C. trivittatus, however, are nearly identical to each other. There is only a slight increase in the means of the ratio between second and third instars and a slight decrease between third and fourth instars.

Because antennal blades are undoubtedly important in capture and ingestion of prey this might suggest differences in progression of prey type from instar to instar between C. trivittatus and C. cooki. However, detailed interpretation of the adaptive significance of this difference must await further study. C. trivittatus larvae (Fedorenko, 1975a, 1975b; Swift, 1976; Swift and Fedorenko, 1975) probably show

closer affinities in prey selection to C. flavicans larvae (Berg, 1937; Dodson, 1970; Parma, 1971b:43; Sikorowa, 1973: Table 18; Swüste et al., 1973) which exhibit allometric change in LB/SB similar to that of C. cooki. However C. cooki, because of the temporary ponds it inhabits, takes quite different types of prey (commonly ostracods, chironomid larvae, culicid larvae). Therefore, an explanation of differing food types does not adequately explain the differences in the pattern of change of LB/SB in C. trivittatus and C. cooki.

4.2.7 Postantennal Filaments

Parma (1971a), Saether (1967, 1970) and Sikorowa (1973) showed no overlap of range between instars in postantennal filament length.

Results for C. trivittatus and C. cooki (Fig. 23B) show that this character is useful to distinguish all individuals of each instar of C. cooki and all, except a few (due to one specimen each) third and fourth instar C. trivittatus. The smallest antennal filament length of fourth instar larvae is from specimens collected 85 km. north of Coleman, Alberta from a high altitude (1975 m) pond which was not shaded. The probably extreme environmental conditions of this habitat possibly produced smaller individuals.

4.2.8 Prelabral Appendages

Parma (1971a:176), Saether (1967: Table 1; 1970:22) and Sikorowa (1973: fig. 9) have shown, in Chaoborus species with laterally flattened prelabral appendages in third and fourth instar larvae, that generally prelabral appendages of third instar larvae

are more slender than are those of fourth instar larvae. This is also true for these instars of C. trivittatus and C. cooki (Fig. 24A). Amount of overlap of PAL/PAW between third and fourth instar larvae is especially pronounced for C. trivittatus.

4.2.9 Number of Mandibular Fan Bristles

This character is useful to identify all specimens to instar in only a few species (Balvay, 1977b; Deonier, 1943; Green, 1972; McGowan, 1972, 1976; Parma, 1971a; Saether, 1967; Sikorowa, 1967b, 1973).

There is some overlap of range in number of mandibular fan bristles between second, third and fourth instar larvae of both C. trivittatus and C. cooki (Fig. 24B) and this character alone can be used only to recognize some second and fourth instars of either C. trivittatus or C. cooki. Range of number of mandibular fan bristles increases in successive instars at a greater rate in C. trivittatus than C. cooki.

4.2.10 Anal Fan Setae

Differences in number of anal fan setae between larval instars have been described for some Chaoborus species by Balvay (1977b), Deonier (1943), McGowan (1972, 1976), Parma (1971a), Saether (1967, 1970), Smith (1960a) and Sikorowa (1973).

Variation of this character for C. trivittatus and C. cooki (Fig. 25A) shows that only some fourth instar larvae of either C. trivittatus or C. cooki can be distinguished using the number of

anal fan setae. First instar larvae may be distinguished from second instar larvae by their paired arrangement of setae (Balvay, 1977b; Parma, 1971a; Sikorowa, 1970, 1973).

4.3 Variation of Characters of Fourth Instar Larvae

4.3.1 Age-related Variation

Age-related variation of fourth instar larvae was studied for C. cooki only. These were collected 1.6 km. south of Jasper on June 4 (n=29) and June 17, 1975 (n=33) with third instar larvae and pupae, respectively. This ensured a sample of fourth instar larvae which exhibited the total age range. Total length was interpreted as representative of age and statistical correlation of the following characters with total length was studied to determine age related variation: antennal length, long antennal blade length, short antennal blade length, LB/SB, LB/AL, distance of antennal seta from antennal base, AS/AL, postantennal filament length, prelabral appendage length and width, PAL/PAW, number of mandibular bristles and number of anal fan setae. Shape of dorsal process was also studied.

Male and female larvae were distinguished using the index described below in the section about sex-associated variation. Probably because of small sample size, female larvae exhibited no characters significantly correlated with body length. Three characters of male larvae were significantly negatively correlated with growth: long antennal blade length, LB/AL, and prelabral appendage length. Because long antennal blade length and antennal length are not correlated to each other in male larvae, the correlation of LB/AL to total length probably reflects the correlation of the long antennal blades to total length. Therefore only two remaining characters are meaningfully related to age. Relationship to total

length of both length of long antennal blade (Fig. 26A) and prelabral appendage length (Fig. 26B) indicates wear with age of these two structures. Wear of long antennal blade is probably associated with prey capture. Roth (1967:66) previously noted wear of prelabral appendages of overwintered C. albatus larvae. Evidence of damage, particularly to the tip of prelabral appendages, producing a blunt tip and therefore a shorter prelabral appendage, is common in fourth instar larvae of C. trivittatus (Fig. 13G), C. cooki and C. nyblaei (Fig. 15A-D). Examination of freshly captured, fluid-preserved material shows that wear of the prelabral appendages is not an artifact of preparation.

Although the drawing of the prelabral appendage of C. nyblaei by Saether (1970: fig. 11G) does not show it, the tip had been broken off and the prelabral appendages of C. nyblaei fourth instar larvae are in fact more elongate (Fig. 15E-H, Hirvenoja, 1961: fig. 2A). The breaking off of the tip of the prelabral appendages of C. trivittatus and C. nyblaei makes them appear similar to those of C. cooki (compare Fig 15C and 14A-F). However, an undamaged prelabral appendage of C. cooki can be separated from damaged ones of C. trivittatus or C. nyblaei through examination of the form of the tip.

4.3.2. Sex-associated Variation

Inclusion of two different groups of semaphoronts in an analysis of variation of characters can result in an overestimation of the amount of intraspecific variation. Characters which display a large degree of sex-associated variation may therefore mistakenly be interpreted as exhibiting a greater degree of intraspecific variation than is actually present, as shown by the following analysis of some characters of fourth instar larvae of C. trivittatus and C. cooki.

Little has been previously reported about larval sex-associated variation of Chaoborus species (Bradshaw, 1973:1249; Smith, 1960a:198, von Frankenberg, 1915:514). Teraguchi and Northcote (1966: fig. 2) give the distribution of head capsule lengths of fourth instar larvae of C. flavicans collected in September which exhibits a bimodality. If this represents male and female larvae, as might be suggested by the results presented below, a comparison of the larvae collected in August and September would suggest that male larvae molt to fourth instar earlier than do females.

4.3.2.1 Chaoborus trivittatus

Statistical comparison of 14 characters (Table 25) of 23 male and 21 female larval exuviae from reared fourth instars collected 2.4 km. west of Edmonton, Alberta on April 26, 1975 indicated that eight characters differed significantly between male and female fourth instar larvae but none without some overlap.

Table 25. Descriptive statistics of male and female fourth larval exuviae of C. trivittatus collected 2.4 km. west of Edmonton, Alberta. Measurements in µm.

Character	Males					Females				
	N	Range	Mean	1.5SD	2SE	N	Range	Mean	1.5SD	2SE
Antennal Length	23	795-899	836	35	10	21	876-1003	935	44	13
Long Antennal Blade Length	23	609-696	660.9	35.4	9.8	21	673-777	723.1	42.3	12.3
Short Antennal Blade Length	23	278-365	321.8	38.5	10.7	21	290-360	324.8	30.4	8.9
LB/SB	23	1.83-2.45	2.06	0.25	0.07	21	2.04-2.52	2.23	0.19	0.06
LB/AL	23	0.68-0.84	0.791	0.053	0.015	21	0.72-0.84	0.773	0.43	0.012
Antennal Seta from Antennal Base	23	702-813	742	37	10	21	783-922	840	49	14
AS/AL	23	0.87-0.91	0.887	0.019	0.005	21	0.86-0.92	0.899	0.024	0.007
Postantennal Filament Length	23	720-791	759	34	9	21	767-885	816	53	12
Prelabral Appendage Length	23	284-447	376.0	70.5	19.6	21	261-464	367.1	82.6	24.0
Prelabral Appendage Width	23	64-87	75.2	10.6	3.0	21	70.93	81.5	12.4	3.6
PAL/PAW	23	3.27-7.00	5.06	1.34	0.37	21	2.81-6.42	4.56	1.39	0.40
No. Anal Fan Setae	23	25-29	27.4	1.4	0.4	21	25.29	27.6	1.6	0.5
No. Mandibular Fan Bristles	23	20-28	22.5	2.6	0.7	21	19-25	22.7	2.4	0.7
Head Capsule Length	20	1676-2100	1949	156	46	19	1900-2313	2116	188	57

To be able to sex larvae without rearing, I constructed a compound character index (Table 26) in which range of variation of head capsule length, antennal length, AS/AL, long antennal blade length, LB/SB, and postantennal length were divided into numbered units with typical male larvae given the lowest unit values and female larvae the highest. Summation of values of each character for each individual showed that male and female larvae can be distinguished if the range of variation of each character in the index is divided into ten units (Fig. 27A). The method, however, depends on a large enough sample to express the bimodality.

4.3.2.2 Chaoborus cooki

Fourth instar larvae of C. cooki were collected 32 km. west of Edson, Alberta on June 5, 1975 and reared to adulthood. Of these, 15 male and nine female larval exuviae were measured for 14 characters and statistically compared (Table 27). Five characters differed significantly between male and female larvae with only postantennal filament length showing no overlap of range. Because of proximity of ranges of postantennal filament length of male and female larvae, this character cannot be used alone to sex larvae which have not been reared. A compound character index was used to sex larvae (Table 28), similar to that described above. Distance of antennal seta from antennal base was not used in the index because it is so markedly correlated to antennal length (Fig. 29B). Resultant index values for individual larvae (Fig. 27B), show larvae can be sexed using this method. Fourth instar larvae used to study growth related variation were also sexed using a compound character index (Table 29). Results (Fig. 27C) were tested by examining distribution of characters used

Table 26. Compound character index used to sex fourth instar larvae of C. trivittatus collected 2.4 km. west of Edmonton, Alberta. Measurements in µm.

Character	Index Value 1	2	3	4	5	6	7	8	9	10
Antennal length	791-815	816-840	841-865	866-890	891-915	916-940	941-965	966-990	991-1015	1016-1040
Long Antennal Blade Length	600-618	619-636	637-654	655-672	673-690	691-708	709-726	727-744	745-762	763-780
LB/SB	1.82-1.89	1.90-1.97	1.98-2.05	2.06-2.13	2.14-2.20	2.21-2.28	2.29-2.36	2.37-2.43	2.44-2.51	2.52-2.59
AS/AL	0.86	0.87	/	0.88	/	0.89	0.90	/	0.91	0.92
Postantennal Filament Length	700-720	721-740	741-760	761-780	781-800	801-820	821-840	841-860	861-880	881-900
Head Capsule Length	1676-1741	1742-1806	1807-1871	1872-1936	1937-2001	2002-2066	2067-2131	2132-2195	2196-2261	2262-2326

Table 27. Descriptive statistics of male and female fourth instar larval exuviae of C. cooki collected 32 km. west of Edson, Alberta. Measurements in µm.

Character	Males					Females				
	N	Range	Mean	1.5SD	2SE	N	Range	Mean	1.5SD	2SE
Antennal length	15	945-1079	1025	67	23	9	1067-1195	1143	66	29
Long Antennal Blade Length	15	487-603	539.4	39.2	13.5	9	551-597	569.0	22.8	10.1
Short Antennal Blade Length	15	354-429	395.6	35.4	12.2	9	377-441	407.9	28.8	12.8
LB/SB	15	1.14-1.51	1.37	0.15	0.05	9	1.36-1.54	1.40	0.09	0.04
LB/AL	15	0.47-0.58	0.527	0.050	0.017	9	0.47-0.56	0.501	0.045	0.020
Antennal Seta from Antennal Base	15	812-951	873	59	20	9	905-1021	907	56	25
AS/AL	15	0.80-0.88	0.851	0.039	0.014	9	0.82-0.88	0.848	0.025	0.011
Postantennal Filament Length	15	649-802	769	61	21	9	826-885	851	29	13
Prelabral Appendage Length	15	206-294	251.2	28.4	9.8	8	229-306	268.2	43.6	20.6
Prelabral Appendage Width	15	59-100	81.9	16.5	5.7	8	71-94	84.5	11.5	5.4
PAL/PAW	15	2.29-4.30	3.13	0.79	0.27	8	2.62-3.43	3.18	0.47	0.22
No. Anal Fan Setae	13	31-36	32.6	2.3	0.9	9	32-35	33.7	1.8	0.8
No. Mandibular Fan Bristles	15	10-15	12.5	1.6	0.5	9	12-14	13.1	1.2	0.5
Head Capsule Length	15	2030-2266	2121	103	36	9	2254-2466	2373	102	45

Table 28. Compound character index used to sex fourth instar larvae of C. cooki collected 32 km. west of Edson. Measurements in µm.

Character	Index Value									
	1	2	3	4	5	6	7	8	9	10
Antennal Length	945-970	971-995	996-1020	1021-1045	1046-1070	1071-1095	1096-1120	1121-1145	1146-1170	1171-1195
Long Antennal Blade Length	487-499	500-510	511-522	521-533	534-545	546-557	558-568	569-580	581-591	592-603
Postantennal Filament Length	649-673	674-696	697-720	721-743	744-767	768-791	792-814	815-838	839-861	862-885
Head Capsule Length	2030-2074	2075-2117	2118-2161	2162-2204	2205-2248	2249-2292	2293-2335	2336-2379	2380-2422	2423-2466

Table 29. Compound character index used to sex fourth instar larvae of C. cooki collected 1.6 km. south of Jasper. Measurements in µm.

Character	Index Value									
	1	2	3	4	5	6	7	8	9	10
Antennal Length	870-906	907-943	944-979	980-1016	1017-1052	1053-1089	1090-1125	1126-1162	1163-1198	1199-1235
Long Antennal Blade Length	539-555	556-572	573-588	589-604	605-620	621-637	638-653	654-669	670-686	687-702
Postantennal Filament Length	731-748	749-764	765-781	782-797	798-814	815-831	832-847	848-864	865-880	881-897
Head Capsule Length	1841-1907	1907-1973	1974-2039	2040-2105	2106-2172	2173-2238	2239-2304	2305-2370	2371-2436	2437-2502

to sex larvae. For example, length of postantennal filaments overlapped only by one specimen between male and female larvae.

It may have been due to smaller sample size used in the analysis of C. cooki that some characters were sex-associated for C. trivittatus larvae but not for those of C. cooki.

4.3.2.3 Chaoborus nyblaei

I did not have reared material of C. nyblaei and was therefore unable to calculate sex-associated variation from fourth instar larvae of known sex. I attempted to sex the larvae by assuming that those larval characters exhibiting sex-associated variation for both C. trivittatus and C. cooki were also sex-associated for C. nyblaei larvae and constructing a compound character index similar to that for the larvae of C. trivittatus and C. cooki, on the basis of head capsule length, antennal length, long antennal blade length, and postantennal filament length. Presumably because of small sample size (n=24) I could not confidently interpret the slight bimodality present in resultant index values.

4.3.3 Correlation of Characters

Analysis of correlation of characters gives important clues on how best to interpret sources of variation, results of compound character indices and characters used in phylogenetic analysis. Ratios which are significantly correlated to another ratio with which they share one character or to one of the characters from which the ratio is composed are presented but most of these correlations are probably artifacts of analysis (Atchley et al., 1976).

Characters of male and female larvae were analyzed separately and this precluded use of specimens of C. nyblaei. However, characters which were significantly correlated for male and female larvae of both C. trivittatus and C. cooki were studied for C. nyblaei fourth instar larvae. Characters were considered significantly correlated at the 95% confidence limit. Because of low numbers of female C. cooki larvae studied, significance or lack of significance may be fortuitous in some comparisons.

The same C. cooki larvae as were studied for age-related variation and C. trivittatus larvae as were used to determine sex-associated variation were studied in this analysis. In addition, the C. cooki larvae studied for sex-associated variation were used to confirm the results from the aforementioned C. cooki larvae. However, because of their greater numbers some characters were significantly correlated for the C. cooki larvae used to determine age-related variation but were not so for the larvae used to study sex-associated variation.

Results for male and female fourth instar larvae of C. trivittatus and C. cooki are given in Figure 28A-D respectively. As for C. trivittatus and C. cooki (Fig. 29A,B), distance of antennal seta from antennal base is strongly correlated to antennal length of fourth instar larvae of C. nyblaei (Fig. 29C).

Correlation between two characters does not necessarily imply a genetic or functional relationship between those characters. However, lack of correlation does suggest a lack of relatedness and I have used only that information in subsequent analyses.

4.3.4 Geographical Variation

Study of geographical variation of characters of fourth instar larvae of C. trivittatus and C. cooki explained some of the large intraspecific variation of some characters, and provided evidence for inferring past distributions. In addition, geographic variation can give supportive evidence of reproductive isolation. Discovery of differences in patterns of geographical variation of head capsule length, AS/AL, and mandibular fan bristles supports the conclusion from other analyses that C. trivittatus and C. cooki are different species.

It is difficult to determine to what extent clines are products of past and present gene flow or environmental gradients. However, analyses of intrapopulational correlation shows which characters are associated, and study of patterns of geographical variation in different areas can indicate which characters are selected independently. Characters such as these, which do in some locations show common patterns, are most likely to reflect gene flow and possibly, historic events.

The geographical variation of seven characters was studied. However, because head capsule length is correlated to antennal length, at least in male larvae, and analysis of antennal length variation showed almost exactly the same pattern as head capsule length for both C. trivittatus and C. cooki, only results of variation of head capsule length are discussed here. Other characters are those used in the compound character index (Fig. 33).

4.3.4.1 Chaoborus trivittatus

I studied 21 samples within Alberta and 14 samples or grouped samples from the rest of North America. Within Alberta, only two areas showed geographical patterns of variation for some of the characters. The samples, numbered 1-5 and 6-9 (Fig. 30), were collected from an area near to or east of Jasper and north of Swan Hills, respectively.

The characters which show a common pattern are head capsule length (Table 30), AS/AL (Table 31), PAL/PAW (Table 32) and number of mandibular fan bristles (Table 33). Generally there is a linear increase or decrease in mean values of samples 1-5 or 6-9 corresponding to the generally linearly arranged set of localities from which samples were collected. Samples 1 and 6 of PAL/PAW do not fit the pattern suggested by other samples or other characters. In addition, direction of clines differs between areas for different characters. Mean values for head capsule length and AS/AL decrease in a west-east direction in the Jasper area and in a north-south direction in the Swan Hills area, while mean number of mandibular fan bristles decrease and PAL/PAW increase in a west-east direction in the Jasper area and south-north direction in the Swan Hills area. While reflecting gene flow, this pattern suggests the non-correlation of local selection of these two character pairs. Lack of patterns of variation of these four characters, particularly in southwestern Alberta (6 samples) is probably due to either a complicating factor or lack of resolution.

Table 30. Variation in head capsule length (in μm) of fourth instar larvae of C. trivittatus in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	1888-2289	2083	236	99
2	11	1699-2207	1985	184	74
3	10	1546-1959	1785	198	83
4	11	1522-2065	1789	276	111
5	25	1487-2077	1702	215	57
6	11	1982-2266	2091	140	56
7	11	1794-2183	1985	200	81
8	12	1746-2199	1946	211	81
9	11	1687-2112	1885	202	82

Table 31. Variation in AS/AL of fourth instar larvae of C. trivittatus in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	0.86-0.92	0.901	0.026	0.012
2	11	0.85-0.92	0.888	0.031	0.012
3	10	0.86-0.91	0.884	0.024	0.010
4	11	0.84.0.91	0.878	0.031	0.012
5	26	0.82-0.92	0.878	0.041	0.011
6	10	0.86-0.92	0.901	0.026	0.011
7	11	0.88-0.92	0.905	0.021	0.008
8	12	0.86-0.92	0.894	0.032	0.012
9	11	0.86-0.91	0.887	0.030	0.012

Table 32. Variation in PAL/PAW of fourth instar larvae of C. trivittatus in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	4.50-7.00	5.263	1.094	0.461
2	11	4.29-5.50	4.983	0.470	0.189
3	10	4.54-5.42	5.002	0.472	0.199
4	11	4.33-6.62	5.288	0.874	0.351
5	26	3.79-6.77	5.442	0.830	0.217
6	11	4.15-6.18	5.075	1.010	0.406
7	11	4.54-7.33	5.847	1.184	0.476
8	12	4.75-9.14	5.656	1.875	0.722
9	11	4.54-7.30	5.558	1.267	0.509

Table 33. Variation in numbers of mandibular fan bristles of fourth instar larvae of C. trivittatus in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	23-29	25.9	2.9	1.2
2	11	16-23	20.0	3.4	1.4
3	10	17-23	19.7	3.7	1.6
4	11	14-21	17.4	3.6	1.4
5	26	12-24	17.2	4.7	1.2
6	11	18-24	21.4	2.7	1.1
7	11	19-25	22.2	3.0	1.2
8	12	18-30	23.0	5.3	2.0
9	11	18-26	22.5	3.2	1.3

Study of six samples or clumped samples from Ontario, Quebec, Newfoundland, Wisconsin and Michigan indicated no apparent patterns of geographical variation, probably because of the few numbers of samples studied from such a large area.

I could distinguish no patterns of geographical variation of head capsule length for samples outside of Alberta but because this character can vary markedly in a relatively small area, as shown above, this was probably due to few numbers of samples. Therefore it may be significant that, of all samples studied, specimens from Klutlane Glacier moraine, Yukon exhibited the highest mean head capsule length (2157 µm).

Two characters, LB/SB and number of anal fan setae did not exhibit geographical patterns within Alberta but did vary geographically on the west coast of North America. At least for number of anal fan setae this discrepancy is explained by the overall homogeneity of samples from Alberta which exhibit, for example, a total range of means in the Jasper region of 27.5-28.1.

Patterns of geographical variation are apparent along the west coast of North America for AS/AL (Table 34), LB/SB (Table 35), PAL/PAW (Table 36), number of mandibular fan bristles (Table 37), and number of anal fan setae (Table 38). Samples are numbered 1-7 (Fig. 31).

Variation in number of mandibular fan bristles and number of anal fan setae exhibit a linear north-south cline with mean values increasing in a northerly direction. Sample 6 of the number of anal fan setae (Table 38) is unexpectedly high, however. The other three characters, AS/AL, LB/SB, and PAL/PAW show a different pattern of

Table 34. Variation in AS/AL of fourth instar larvae of C. trivittatus from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	0.83-0.90	0.863	0.033	0.015
2	15	0.86-0.92	0.891	0.027	0.009
3	10	0.89-0.93	0.911	0.019	0.008
4	14	0.89-0.92	0.908	0.018	0.006
5	10	0.85-0.91	0.887	0.025	0.010
6	12	0.87-0.92	0.890	0.023	0.009
7	13	0.84-0.92	0.890	0.035	0.013

Table 35. Variation in LB/SB of fourth instar larvae of C. trivittatus from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	8	1.76-2.18	2.040	0.200	0.94
2	15	1.80-2.49	2.110	0.280	0.097
3	10	2.39-2.81	2.510	0.222	0.094
4	14	2.12-2.92	2.530	0.272	0.097
5	10	1.95-2.44	2.240	0.249	0.105
6	12	1.47-2.34	2.040	0.334	0.129
7	12	1.85-2.37	2.080	0.236	0.091

Table 36. Variation in PAL/PAW of fourth instar larvae of C. trivittatus from west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	2.63-6.36	4.739	1.717	0.763
2	14	4.14-6.09	5.060	0.702	0.250
3	10	4.18-6.25	5.172	0.953	0.402
4	14	3.82-5.83	4.477	0.847	0.302
5	10	3.27-6.80	5.553	1.496	0.631
6	12	4.25-6.67	4.992	1.199	0.462
7	13	3.30-6.25	4.832	1.482	0.548

Table 37. Variation in numbers of mandibular fan bristles of fourth instar larvae of C. trivittatus from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	11	18.33	27.7	6.6	2.6
2	15	21-36	26.2	6.1	2.1
3	10	22-29	24.7	4.2	1.8
4	14	20-32	25.5	4.2	1.5
5	10	20-29	24.0	3.9	1.7
6	12	21-30	23.8	3.7	1.4
7	16	18-31	22.3	5.8	1.9

Table 38. Variation in numbers of anal fan setae of fourth instar larvae of C. trivittatus from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	31-33	32.0	1.3	0.6
2	15	27-31	28.6	2.0	0.7
3	10	26-38	27.4	1.0	0.4
4	14	26-29	27.9	1.3	0.5
5	10	25-29	27.0	1.9	0.8
6	12	27-30	28.4	1.4	0.5
7	12	25-30	27.1	2.1	0.8

variation with the highest mean values near the middle of the cline in the Washington or southwestern British Columbia region. None of these three characters shows any intrapopulational correlation. In addition, study of AS/AL and PAL/PAW in Alberta shows that at least these two characters are selected for independently. Therefore, concurrent patterns of geographical variation of these three characters probably evidence the historic events discussed below.

It seems likely, considering the present distribution of C. trivittatus that this species was able to survive in both the Alaskan-Yukon refugium, and the refugia and that south of the continental ice sheet during the Wisconsonian glaciation. Because C. trivittatus is now restricted to woodland conditions (pg. 49), discovery of woodland in parts of the Beringian refugium (Hopkins, 1972) would additionally suggest that C. trivittatus could have survived in this region.

This inferred distribution during the Wisconsonian glaciation adequately explains some geographic variation. Even if an ice free corridor was present in Alberta (Reeves, 1973) and the Alaskan-Yukon refugial population was not reproductively isolated from some populations south of the continental ice sheet, this would not affect the argument presented here. Geographical patterns of variation along the west coast of North America would, regardless of a more westerly corridor, be the result of resumed reproduction between northern and southern populations along the west coast as the continental ice retreated (Prest, 1969).

The Yukon sample, from a pond on Klutlane Glacier moraine, exhibits the extreme of clinal variation of five characters (AS/AL, LB/SB, PAL/PAW, number of mandibular fan bristles, number of anal fan setae). These patterns are consistent with a hypothesis suggesting the

past isolation of this population (see below).

Johnson (1977) has recently suggested that coastal California had a similar climate during the last continental glaciation as it has now. There is little doubt that C. trivittatus populations were present in the region at that time. It would be reasonable to suggest that clinal variation of AS/AL, LB/SB and PAL/PAW along the west coast of the United States (i.e. south of the area formerly occupied by the continental ice sheet) is similar to that during the Wisconsonian glaciation. Probably the peak of mean values of AS/AL, LB/SB, and PAL/PAW in Washington or southwestern British Columbia represents the northern end of clinal variation of past populations. Subsequent retreat of the continental ice opened a coastal corridor and allowed contact between populations from the Alaskan-Yukon refugium and those immediately south of the ice sheet, thereby resulting in intermediate clinal values (Prince Rupert sample).

4.3.4.2 Chaoborus cooki

I studied seven samples, numbered 1-7 (Fig. 32), of fourth instar larvae of C. cooki in Alberta. Two additional samples from the Yukon, from along the Dempster Highway and from a pond on Klutlane Glacier moraine, were so similar to each other and distant from the Alberta samples that I did not include them in this description.

A common geographical pattern is evident for four characters: head capsule length (Table 39), AS/AL (Table 40), number of mandibular fan bristles (Table 41) and number of anal fan setae (Table 42). Of the three samples near Jasper, sample 3 is closest geographically to sample 5. Samples 2, 3 and 4 are, although not in

Table 39. Variation in head capsule length (in μm) of fourth instar larvae of C. cooki. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	12	2148-2620	2396	204	79
2	10	1888-2360	2153	228	96
3	63	1841-2502	2153	217	37
4	17	1841-2325	2027	223	72
5	27	1770-2466	2178	260	67
6	13	2030-2443	2216	230	85
7	8	2065-2466	2304	236	111

Table 40. Variation in AS/AL of fourth instar larvae of C. cooki. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	12	0.81-0.89	0.856	0.038	0.014
2	11	0.81-0.89	0.850	0.035	0.014
3	62	0.80-0.89	0.851	0.031	0.005
4	17	0.81-0.87	0.832	0.023	0.007
5	27	0.80-0.90	0.854	0.038	0.010
6	13	0.80-0.93	0.866	0.046	0.017
7	8	0.83-0.88	0.864	0.025	0.012

Table 41. Variation in numbers of mandibular fan bristles of fourth instar larvae of C. cooki. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	14	13-21	15.4	2.9	1.0
2	11	11-14	12.9	1.4	0.6
3	62	11-15	13.5	1.5	0.3
4	17	12-17	13.9	2.0	0.7
5	27	10-15	12.9	1.6	0.4
6	13	12-16	13.8	1.6	0.6
7	8	13-17	14.5	2.1	1.0

Table 42. Variation in numbers of anal fan setae of fourth instar larvae of C. cooki. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	13	31-36	33.3	2.1	0.8
2	11	32-38	33.8	2.7	1.1
3	61	28-36	32.8	2.4	0.4
4	17	30-34	31.9	1.6	0.5
5	25	31-36	32.9	2.2	0.6
6	14	31-34	33.0	1.4	0.5
7	8	30-35	32.2	3.1	1.5

a straight line geographically, probably linearly arranged in terms of dispersal of this species along a continuous valley bordered, except to the eastward side of sample 3, by high mountains.

The pattern of geographical variation for the characters is similar. Sample 1 evidences the highest average for all four characters with the exception of AS/AL. The three Jasper samples, 2, 3 and 4 show a successive increase and decrease in mean value of number of mandibular fan bristles and number of anal fan setae, respectively. There is generally a successive increase of mean values of head capsule length, AS/AL, number of mandibular fan bristles and number of anal fan setae for samples 3, 5, 6 and 7. However, the following are exceptions to this pattern. Sample 5 mean number of mandibular fan bristles is less than that of sample 3. For AS/AL, the mean value of sample 6 is nearly identical to that of sample 7. For number of anal fan setae, the mean values of samples 5, 6 and 7 show no significant change.

Nevertheless, these overall patterns show that some of the greater differences among means may be attributable to this source. In addition, variation of number of anal fan setae of samples 2, 3 and 4 shows that characters vary significantly in a small geographic area and therefore suggests either strong local selection or restricted gene flow between populations.

4.3.5 Compound Character Index and Characters Differing Between Fourth Instar Larvae of Species of Schadonophasma

Initially I had difficulty distinguishing between fourth instar larvae of C. trivittatus and C. cooki. Although I could identify some populations using characters described by Saether (1970), I found variation of all individual characters to present a confusing continuum (see Fig. 21-25A) and was uncertain which characters could, in combination, be used to identify members of these two species. I therefore compared reared material of both sexes of C. trivittatus and C. cooki used in analysis of sex-associated variation to discover which characters might differ between the two species. Characters examined in the study of sex-associated variation differed significantly except length of postantennal filaments (see Tables 25, 27) between male larvae, and prelabral appendage width between female larvae. Identifications were confirmed through examination of associated adults.

For the purpose of this study I treated these two samples as if they were sympatric. Testing for species differences through initial comparison of samples collected from the same locality reduces differences due to geographic and ecotypic variation. However, such samples were not available to me when I initiated this study.

Six characters which differed between both males and females of C. trivittatus and C. cooki and not correlated to each other were chosen from which to construct a compound character index to give single values for individual specimens summarizing their features (Table 43). The correlation between LB/SB and AS/AL for C. cooki

Table 43. Compound character index used to recognize fourth instar larvae of Chaoborus trivittatus and Chaoborus cooki. Measurements in μm.

Character	Index Value																			
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Antennal Length	1185-1210	1159-1184	1133-1158	1107-1132	1081-1106	1055-1080	1029-1054	1003-1028	977-1002	951-976	925-950	899-924	873-898	847-872	821-846	795-820	769-794	743-768	717-742	691-716	665-690
LB/SB	1.08-1.15	1.16-1.23	1.24-1.31	1.32-1.39	1.40-1.47	1.48-1.55	1.56-1.63	1.64-1.71	1.72-1.79	1.80-1.87	1.88-1.95	1.96-2.03	2.04-2.11	2.12-2.19	2.20-2.27	2.28-2.35	2.36-2.43	2.44-2.51	2.52-2.59	2.60-2.67	2.68-2.75
AS/AL	.75	.76	.77	.78	.79	--	.80	.81	.82	.83	.84	.85	.86	.87	.88	--	.89	.90	.91	.92	.93
PAL/PAW	1.70-2.05	2.06-2.41	2.42-2.77	2.78-3.13	3.14-3.49	3.50-3.85	3.86-4.21	4.22-4.57	4.58-4.93	4.94-5.29	5.30-5.65	5.66-6.01	6.02-6.37	6.38-6.73	6.74-7.09	7.10-7.45	7.46-7.81	7.82-8.17	8.18-8.53	8.54-8.89	8.90-9.25
No. Mandibular Fan Bristles	8,9	10	11	12	13,14	15	16	17	18,19	20	21	22	23,24	25	26	27	28,29	30	31	32	33,34
No. Anal Fan Setae	40	39	38	37	36	—	35	34	33	32	31	30	29	28	27	--	26	25	24	23	22

females and between PAL/PAW and number of mandibular fan bristles of male C. cooki were considered to be unimportant, especially as the correlation did not appear in the opposite sex of C. cooki or in either sex of C. trivittatus.

Range of each character was divided into 21 equal units numbered 0-20. The number 0 represented the extreme of C. cooki variation of a character and number 20 the opposite extreme of C. trivittatus variation. C. cooki larvae would therefore receive overall lower final index values than those of C. trivittatus. To compare all Schadonophasma species the index, although based on differences between C. trivittatus and C. cooki, included the variation of C. nyblaei. Consequently the lowest index values of the number of mandibular fan bristles and two of the lowest values of number of anal fan setae represent extremes of C. nyblaei variation.

The values of two specimens of C. trivittatus went beyond the recorded range of LB/SB and one each beyond the range of PAL/PAW and number of mandibular fan bristles. These specimens were given the highest index value for that character. It seems unlikely that these changes in procedure significantly affected the final results.

The distribution of index values for both C. trivittatus and C. cooki fourth instar larvae (Fig. 33) shows that almost all specimens can be identified with confidence. In addition, if more than seven specimens are examined, range of means of compound character values of C. cooki (34.0-43.3) and C. trivittatus (63.8-81.0) allows identification of all samples. Although one character was sex-associated for C. cooki and three for C. trivittatus, there was no significant difference between index

values of male and female C. trivittatus. There was a significant difference between index values of male and female larvae of C. cooki but with a large degree of overlap. I therefore did not consider it important to separate male and female larvae. In addition, most samples were too small to confidently distinguish male and female larvae using a compound character index.

C. nyblaei fourth instar larvae (n=20) index values had a range of 16-47, mean of 36.4, 1.5SD of 11.6 and 2SE of 3.6. Therefore C. nyblaei fourth instar larvae can be distinguished from those of C. trivittatus but not from those of C. cooki using this index.

Specimens from Russell Lake, Alberta (n=10, range = 43-57, mean = 52.3, 1.5SD = 7.1, 2SE = 3.0), from Mechant Lake, Quebec (n=11, range = 50-62, mean = 57.1, 1.5SD = 6.8, 2SE = 2.7) and from Gallienne Lake, Quebec (n=19, range = 45-66, mean = 55.3, 1.5SD = 8.4, 2SE = 2.6) exhibited intermediate index values and could therefore not be identified. These samples are described and discussed below under 'Populations incertae sedis'.

Mean index values did not exhibit geographical patterns of variation. This was probably partially the result of independent patterns of geographical variation of individual characters evidenced, for example, by some characters of C. trivittatus larvae in Alberta.

On the basis of the above results I could determine that variation of each character for all samples studied, although with overlap, differed significantly between fourth instar larvae of C. trivittatus and C. cooki (Fig. 21-25A);(Table 6, 15). Fourth instar larvae of C. nyblaei were significantly different in all characters from those of C. trivittatus but were only significantly

different from those of C. cooki in postantennal filament length, number of mandibular fan bristles and number of anal fan setae. Both second and third instar larvae of C. trivittatus and C. cooki differed significantly for each character studied. First instars differed in all characters except LB/AL and postantennal filament length.

Saether (1970:21) recognized number of mandibular fan bristles (23-32), LB/SB (1.8-2.3) and LB/AL (0.70-0.79) as diagnostic for C. brunskilli fourth instar larvae. However, it is clear from the distribution of these characters of larvae of C. trivittatus (Fig. 34A-C) that these characters do not exhibit any bimodality suggestive of another species and cannot be used to distinguish the larvae of named C. brunskilli as members of a separate taxon.

Because some species of Chaoborus exhibit a limited range of number of mandibular fan bristles Saether (1970:18) argued that 'At least it seems very unlikely that a variation of 11-32 setae, the total variation within Schadanophasma (sic), may be accounted for by the presence of only one or two species'. I can see no justification for such an argument. Determination of a large range of variation of a character, such as the number of mandibular fan bristles of C. trivittatus reported here, is not a valid criterion for suspecting the presence of more than one species.

4.4 Variation of Characters of Pupae

Pupal material was identified on the basis of reared material, association with known larvae, on the basis of distribution of the species, or observations of pharate adult characters.

The most detailed, recent description of pupae of all species of Schadonophasma has been provided by Saether (1970). All material was correctly identified with the exception of the pupae of C. brunskilli (= C. trivittatus). The pupa from Stanford, California was not reexamined but the locality from which it was collected and its association with larvae of C. trivittatus shows clearly that this specimen was correctly identified.

Saether (1970), however, did not take into account the marked sex-associated variation. His description of C. cooki pupae included four males, of C. brunskilli (= C. trivittatus) one male, and of C. nyblaei two males and ten females. The sex of the pupa of C. trivittatus is not known but that Saether (1970) recorded genital sac length only for male pupae and did not do so for this specimen suggests it was a female.

Descriptive statistics for both sexes of each species for most characters described below are given in the species descriptions and comparison of that data shows only those characters presented in the keys to be useful for species determination.

Because of the small size of individual samples, to estimate sex associated variation of C. trivittatus and C. cooki pupae I compared all males with all females within each species. Compared material of C. nyblaei was from a single locality. Seven characters

were studied: abdomen length, length, width and length/width of respiratory horns and length, width and width/length of abdominal segment seven. The shape and size of the genital lobes differs markedly between male and female Chaoborus pupae (Fig. 2C,D; Deonier, 1943: fig. 1,2). In addition, female pupae are slightly darker in overall coloration than males collected from a single locality.

Five characters were sex associated in pupae of C. trivittatus: length and width of respiratory horns, length and width of abdominal segment seven, and total abdominal length. Length, width and length/width of the respiratory horns and length and width of abdominal segment seven were sex associated for pupae of C. cooki; for pupae of C. nyblaei length and width of respiratory horns, length, width and width/length of abdominal segment seven, and total abdominal length were sex-associated.

It is reasonable to assume that the length and width measurements are sex-associated because of a difference in overall size of male and female pupae. Total abdominal length is sex-associated in pupae of C. trivittatus but not in those of C. cooki. This probably reflects stage of development of eggs, which may distend the abdomen and are more developed in older female pupae of C. trivittatus than in C. cooki. Because this character is sex-associated for pupae of C. nyblaei this suggests that ovaries of this species develop in a similar fashion to C. trivittatus.

Saether (1970:18) noted that width/length of abdominal segment VII (erroneously stated as VIII) is 1.4 for C. trivittatus, 1.5 for C. brunskilli (= C. trivittatus), 1.6 for C. cooki, and 1.7-1.9 for C. nyblaei pupae. Examination of Tables 4, 5, 13, 14, 20 and 21 shows extensive overlap of range of this character between males or females of each species.

Coloration differences noted by Saether (1970) were unreliable when more material was examined. There is little doubt that ethanol preserved specimens lose at least some of their color with time. In addition, Saether (1967) has shown that coloration of the anal paddle ribs varies extensively within pupae of C. flavicans. However, his results may be biased through the use of specimens treated with KOH.

Differences of the angle of the abdomen in relation to the longitudinal axis of the body between pupae of C. trivittatus and C. cooki (Fig. 5A,B) were observed from most of the samples as they were collected and/or reared in the laboratory, from localities in Alberta during the course of this study. The character was consistent for identification of pupae examined.

Differences in development of ovaries of pupae of C. trivittatus and C. cooki were apparent (see key to female pupae) and this trait is also expressed in the stage of ovarian development in teneral female adults (see below). In live female pupae of C. trivittatus at least 48 hours old (at 20°C) ovaries are macroscopically apparent as white elongate organs in the abdomen (see Parma, 1971b:40). These are not apparent in female pupae of C. cooki.

4.5 Variation of Characters of Male Adults

Saether (1970) noted two characters of diagnostic value for determination of adult males to species: shape of penis valves and X/Y wing ratio. These two characters were studied in detail. Other differences between males of the three species of Schadonophasma are available by comparison of the descriptions (Table 1, 9). Characters differing significantly between male adults of C. trivittatus and C. cooki are Rsa length, all leg measurements, basistyle and dististyle length, Y/X, number of tergum IX setae and penis valve length.

Differences in coloration of adults of C. trivittatus and C. cooki (see descriptions) may in part be ecophenotypic. Bradshaw (1973:1256) mentions that male adult C. americanus are a darker color when reared at temperatures below 15°C and this may also have an effect on color variation of adult Schadonophasma (also see Rapoport, 1969; Vernberg, 1962).

Range of variation of Y/X of male adults of C. trivittatus (Table 2) and C. cooki (Table 11), although significantly different, exhibits extensive overlap. Range of variation of Y/X of C. nyblaei male adults (see description) is within the range of Y/X of both C. trivittatus and C. cooki.

I studied geographical variation of this character for C. trivittatus and C. cooki but, possibly because of the small number of samples, recognized no patterns. However, it is clear that the ratio, at least for C. trivittatus, varies markedly in a relatively small geographical area. A sample from 16 km. west of Jasper, Alberta

(n=38, range = 1.35-2.18, mean = 1.705, 1.5SD = 0.310, 2SE = 0.067) differed significantly from a sample 2.4 km. west of Edmonton, Alberta (n=40, range = 1.54-2.42, mean = 1.915, 1.5SD = 0.309, 2SE = 0.065).

Saether (1970) distinguished four types of penis valves characteristic of each of the four species he described. Apparently because of the similarity of penis valves of the male from Baffin Island with those of the specimen from Finland, he identified the former specimen as C. nyblaei. In addition, differences in the penis valves of the male from Lk. 241, Kenora, Ontario supported his recognition of the larvae from that area as indicative of the new species C. brunskilli. However, these penis valves were not examined in a standard orientation. Reorientation of the penis valves of the specimens from Baffin Island and Lk. 241, Kenora resulted in forms indistinguishable from those typical of C. trivittatus. The dark, very short tips of the penis valves of C. nyblaei as drawn by Saether (1970: fig. 7A,B) are actually the claws pointing downward. Outlines of a single penis valve of a male C. trivittatus (Fig. 12A-E) drawn from different perspectives shows that one orientation (Fig. 12D) is very similar to that thought by Saether (1970: fig. 7A,B) to be typical of C. nyblaei and another (Fig. 12B) typical of C. brunskilli (Saether, 1970: fig. 7C). The effect of changed orientations of a single penis valve of C. cooki (Fig. 12F-J) shows the importance of examining the penis valves from different orientations. For example, one orientation of the valve of a male of C. cooki (Fig. 12F), is extremely similar to one orientation of the penis valve of C. trivittatus (Fig. 12A). For the purposes of this study only Figures 12E and 12H

show useful orientations. Of the material I examined, no penis valves of C. trivittatus looked like thos of C. cooki when in this orientation.

The two types of penis valves recognized by Saether (1970:27) to be typical of two forms of C. americanus are also a result of examination of material from different perspectives (pers. obs.)

Because of the seemingly impossible prospects of completely standard orientation of penis valves, even though all specimens were drawn with the penis valve head in a horizontal plane, it is not known to what degree this affected the drawings of intraspecific and interspecific variation of penis valves of C. trivittatus (Fig. 10A-O) and C. cooki (Fig. 11A-N). Although a comparison between amount of intrapopulational and interpopulational variation of penis valves of either C. trivittatus or C. cooki do not show very marked differences in these figures, there is actually more interpopulational than intrapopulational variation.

The penis valves of male C. nyblaei are illustrated in Figure 11 O,P.

Length of penis valves differed significantly between C. trivittatus and C. cooki even though the entire range of variation of that of C. cooki was contained in the range of variation of length of penis valves of C. trivittatus. Length of penis valves of C. nyblaei was within the range of both C. cooki and C. trivittatus.

The only apparent pattern of geographical variation of the length of penis valves was for C. trivittatus along the west coast of North America (Table 44). Although this linear increase in mean values cannot be confidently interpreted on its own, geographical variation in five larval characters in this region suggests that the

Table 44. Variation of penis valve length (in μm) of male adult C. trivittatus. Sample 1 from Pacific Grove, Stanford, Oakland and Mad River Beach, California. Sample 2 from Hoodsport, Port Madison and Bremerton, Washington and Kaslo, British Columbia. Sample 3 from Prince Rupert and Terrace, British Columbia.

Sample	N	Range	Mean	1.5SD	2SE
1	9	145-191	167.6	20.6	9.2
2	14	162-209	180.6	17.7	6.3
3	8	168-197	190.0	14.5	6.8

pattern is significant (see section on geographical variation of fourth instar larvae).

Number of setae on one side of tergum IX was studied only because it was convenient to do so when examining penis valves. Saether (1970) has already shown large amount of overlap of variation of this character between C. trivittatus and C. cooki, although analysis here does indicate them to be significantly different. I could detect no patterns of geographical variation of this character for either species.

4.6 Variation of Characters of Female Adults

The only diagnostic feature of females given by Saether (1970) was Y/X wing ratio of C. trivittatus and C. cooki. Female adults were not available for C. nyblaei.

I identified females on the basis of their temporal and geographical association with males, geographical distribution or, type of ovarian development and egg type. I studied only variation of Y/X wing ratio in detail. Other differences between females of these species are in the descriptions. Characters which differed significantly between C. trivittatus and C. cooki were length of penultimate antennal article, prementum length, HW/PL, number of anepisternal setae, all leg measurements, and seminal capsule diameter. Number of setae on the comb of the third tarsomere of either midleg or hindleg has not been previously recorded but was found to differ significantly between the two species.

Although means of the ratio Y/X of female adult C. trivittatus and C. cooki differ significantly, ranges overlap extensively (Table 3, 12). Mean values did not exhibit geographical patterns of variation. Similar to males, this character of females can vary markedly in a relatively short distance. A sample from 16 km. west of Jasper (n=10, range = 2.03-2.86, mean = 2.414, 1.5SD = 0.425, 2SE = 0.179) differed significantly from a sample 2.4 km. west of Edmonton, Alberta (n=28, range =1.57-3.22, mean = 2.267, 1.5SD = 0.538, 2SE = 0.136). However, a sample from eight localities in California (n=19, range = 1.19-2.95, mean = 1.919, 1.5SD = 0.653, 2SE = 0.200) did not differ significantly from

a sample from Terrace and Atlin, British Columbia and Whitehorse, Yukon (n=15, range = 1.46-2.56, mean = 2.011, 1.5SD = 0.444, 2SE = 0.153).

Females of C. trivittatus and C. cooki differ in ovarial development. Female C. trivittatus less than one hour old reared from fourth instar larvae collected 2.4 km. west of Edmonton, Alberta, had abdomens full of eggs with ovaries of some extended into the thorax. A ratio of distance of the anterior tip of the longest ovary from the end of the abdomen/abdominal length was 0.71-1.11 (mean = 0.967). The ovaries together contained 251-329 (mean = 279) eggs which at this stage were each at least 348 µm long. Fedorenko (1975c:3102) recorded 161 ± 7.4 SE eggs per female pupae from Eunice Lake, British Columbia.

Females of C. cooki less than 12 hours old, collected as early instars 1.6 km. south of Jasper or as fourth instar larvae 1.4 km. west of George Lake, Alberta, had much smaller ovaries with a ratio of the distance of the anterior tip of the longest ovary from the tip of the abdomen/abdominal length of 0.32-0.62 (mean = 0.444). Total number of eggs present was 74-95 (mean = 86). Each egg in a teneral female is no more than 120 µm long. Teneral females of these two species can therefore be distinguished from one another by size of ovaries. A nulliparous female can be identified by number of eggs present. If an individual with at least some eggs present is suspected of being parous, the eggs are developed enough to distinguish the type of egg. A thick exochorion is typical of C. cooki (Fig. 9C) and a thin exochorion is typical of C. trivittatus eggs (Fig. 9A).

I had available only two females of C. nyblaei which still had eggs in their abdomens. One was the lectotype and its abdomen contained eggs with a thick exochorion (Fig. 9B). I did not count the number of eggs present. The other female, from Abisko, Sweden, had the same type of egg and its abdomen contained 58 eggs. Implications of differences in egg type are discussed below in the section on development of eggs.

4.7 Descriptions of Populations Incertae Sedis

Three samples of larvae and one sample of pupae could not be identified with certainty. The three larval samples exhibited compound character index values (see pg. 127) intermediate between those of C. trivittatus and C. cooki. Although the two samples from Mechant and Gallienne Lakes, Quebec are here described separately, they possibly belong to the same reproductive population, considering the close proximity of the lakes. Pope et al. (1973) recognized samples from these two lakes as members of a new species or subspecies of Schadonophasma but did not describe them.

Several interpretations of these samples seem equally reasonable. Individuals may belong to one or more new species or they may be hybrids between C. trivittatus and C. cooki, although number of specimens would seem too large to be the product of hybridization (see section on mating experiments). Also, specimens may be members of C. cooki. Data from the sample from Russell Lake, Alberta, shape of prelabral appendages of all larvae of all samples and shape of penis valves of pupae from Gallienne Lake, Quebec suggests the likelihood of this (see below for details). None of the specimens in the analysis of C. cooki came from lakes. C. cooki may occasionally invade this habitat and resultant individuals may therefore be phenotypically different from individuals of C. cooki described in this study. Sikorowa (1973) has shown that habitat influences variation of characters of larvae of C. flavicans. Examination of adults, study of geographical variation once more material is

available, especially from eastern Canada, study of the life cycle, and developmental studies could be used to test this possibility.

4.7.1 Sample from Russell Lake, Alberta

All specimens collected 1-VIII-1969, were fourth instar larvae. The population from which this sample was taken is within the geographical range of both C. trivittatus and C. cooki. Coloration is as other members of the subgenus. Measurements and proportions are given in Table 45.

Variation of most characters gave no clues whether this sample might be composed of larvae of either C. trivittatus or C. cooki or of a third undescribed species because the range of these characters was within the range of variation of both C. trivittatus and C. cooki. Low PAL/PAW values would suggest the sample is conspecific with C. cooki. However, some specimens exhibit LB/AL values, number of mandibular fan bristles, and number of anal fan setae which are beyond the range of C. cooki and into the range of variation of C. trivittatus.

All characters were examined in relation to clinal variation of these characters of both C. trivittatus and C. cooki for clues of conspecificity. Only mean number of mandibular fan bristles may possibly be explained by clinal variation of this character of C. cooki fourth instar larvae.

4.7.2 Sample from Mechant Lake, Quebec

All specimens were collected 14-VII-1975 as fourth instar larvae. Although Pope et al. (1973) report that a population represented by this sample coexisted with larvae of C. trivittatus,

Table 45. Descriptive statistics for fourth instar larvae of Schadonophasma from Russell Lake, Alberta. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	13	1884-2060	1975	94	35
Antennal length	12	835-947	913	52	20
LB/SB	10	1.71-2.12	1.91	0.18	0.07
LB/AL	12	0.74-0.91	0.800	0.075	0.029
AS/AL	12	0.79-0.90	0.847	0.053	0.020
Postantennal filament length	13	761-882	829	55	21
PAL/PAW	13	1.76-2.44	2.09	0.29	0.11
No. mandibular fan bristles	13	15-19	17.5	1.8	0.7
No. anal fan setae	13	27-30	28.9	1.6	0.6

I did not examine any material of C. trivittatus which would have given better clues concerning possibilities of the two being conspecific. However the recognition of two forms in a single lake does not negate possibilities of forms being conspecific. Fedorenko and Swift (1972) described two forms of C. trivittatus which differed in size and color but merely represented two overlapping generations.

Larvae are darker than any other Chaoborus larvae I have examined. Head capsules were notably darker in coloration. In particular dorsum of head capsule, area around the anterior pits and dorsal from each pit to dorsum of head capsule, posterior edge of head capsule including ocular-antennal segment, ventral edge of head capsule between antennae and labrum, antennae, maxillary palpus and seta, and anal fan setae were all more darkly pigmented. All thoracic and abdominal segments were infuscated dorsally. Measurements and proportions are given in Table 46.

Some individuals have AS/AL and PAL/PAW values within the range of C. cooki and beyond the range of C. trivittatus. Conversely, some individuals exhibited head capsule length, antennal length, LB/SB, LB/AL, and number of mandibular fan bristles within the range of variation of those characters of C. trivittatus beyond the range of those of C. cooki.

4.7.3 Sample from Gallienne Lake, Quebec

All specimens were collected 13-VIII-1971 as fourth instar larvae. Color of larvae was similar to that of larvae from Mechant Lake, Quebec. For measurements and proportions see Table 47.

Table 46. Descriptive statistics for fourth instar larvae of Schadonophasma from Mechant Lake, Quebec. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	11	16-7-1782	1682	71	29
Antennal length	11	731-777	757	24	10
LB/SB	11	1.71-2.15	1.99	0.13	0.05
LB/AL	11	0.79-0.91	0.843	0.046	0.019
AS/AL	11	0.77-0.89	0.841	0.054	0.022
Postantennal filament length	11	637-708	687	31	12
PAL/PAW	11	2.50-3.08	2.82	0.28	0.11
No. mandibular fan bristles	11	12-15	13.2	1.5	0.6
No. anal fan setae	11	26-29	27.5	1.6	0.6

Table 47. Descriptive statistics for fourth instar larvae of Schadonophasma from Gallienne Lake, Quebec. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	19	1876-2183	2029	142	42
Antennal length	19	824-974	908	66	20
LB/SB	19	1.85-2.27	2.08	0.21	0.06
LB/AL	19	0.75-0.86	0.810	0.052	0.016
AS/AL	19	0.75-0.91	0.843	0.059	0.018
Postantennal filament length	19	743-861	809	51	12
PAL/PAW	19	1.71-4.00	2.67	0.68	0.21
No. mandibular fan bristles	20	13-17	15.4	1.5	0.4
No. anal fan setae	20	25-29	27.2	1.9	0.6

Some individuals exhibited LB/SB, LB/AL ratios and number of anal fan setae beyond the range of variation of these characters for C. cooki but within the range of those of C. trivittatus. Prelabral appendages were typical of those of C. cooki larvae. Head capsule, antennal and postantennal filament length and number of mandibular fan bristles of this sample differed significantly from those of larvae from Mechant Lake. However, this might be explained by geographical variation or differences in habitat. No ratios significantly differed between the two samples.

Pupae were darker than any other Chaoborus material examined. Measurements and proportions of male pupae are given in Table 48 and of female pupae in Table 49. Nearly all measurements of both male and female pupae were within or less than the range of variation of C. trivittatus. Only the WS/LS of male pupae was within the range of WS/LS of both C. trivittatus and C. cooki.

Penis valves were developed in three male pupae but because these could not be removed to study from different orientations without destroying the rest of the specimen, were difficult to interpret. Penis valves of one of these individuals were most similar to those of C. cooki adults. However, length of penis valves ranged from 156.6-162.4 µm. Because material had been previously cleared I could not determine the degree of ovarian development of two pharate female adults. One specimen had well developed seminal capsules with a diameter of 50.0 µm.

Table 48. Descriptive statistics for male pupae of Schadonophasma from Gallienne Lake, Quebec. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdominal length (mm.)	4	5.5-5.9	5.72		
Respiratory horn length (mm.)	4	1.06-1.23	1.112		
Respiratory horn width (mm.)	4	0.30-0.32	0.307		
Abdominal segment VII length	9	767-885	821	62	28
Abdominal segment VII width	4	1133-1263	1192		
WS/LS	4	1.45-1.49	1.48		

Table 49. Descriptive statistics for female pupae of Schadonophasma from Gallienne Lake, Quebec. Measurements in µm unless otherwise given.

Character	N	Range	Mean	1.5SD	2SE
Total abdominal length (mm.)	8	4.3-5.6	4.81	0.61	0.29
Respiratory horn length (mm.)	3	1.07-1.17	1.117		
Respiratory horn width (mm.)	4	0.27-0.31	0.289		
Abdominal segment VII length	9	814-885	852	40	18
Abdominal segment VII width	8	979-1227	1136	116	55
WS/LS	8	1.20-1.42	1.32	0.098	0.046

5. Bionomics and Behavior

Studies of life histories, developmental characteristics and behavior give important information on questions of conspecificity, suggest how species closely related evolutionarily retain their reproductive unity, and are important in interpretation of characters used to infer evolutionary history of such species and the events pertaining thereto. In this section I present observations made on C. trivittatus and C. cooki in Alberta. These are used to infer some probable bionomic features of C. nyblaei in Fennoscandia. For the following analysis observations were made of events which I had the opportunity and time to deal with and which I believed to be most informative to elucidate species differences and evolution. A more complete, general account of such bionomic information has been presented by Parma (1971b).

5.1 Life Cycle

All temperate Chaoborus species previously studied exhibit a life cycle in which fourth instar larvae overwinter, pupate in spring, emerge as adults which lay eggs and develop to fourth instar larvae by winter (Balvay, 1977d; Bradshaw, 1973; Fedorenko and Swift, 1972; Parma, 1971b; Sikorowa, 1973). In multivoltine populations these fourth instar larvae result in another adult emergence and subsequent larvae, but regardless of number of generations per year, every temperate species studied overwinters as fourth instar larvae. For this reason,

immatures of these species are usually present only in permanent waters. Studies of tropical species (Corbet, 1958; Lewis, 1975; MacDonald, 1956; McGowan, 1974, 1975; Tjønneland, 1958; Verbeke, 1957) suggest that these are also restricted to permanent waters. Records of Chaoborus larvae in temporary waters in the tropics (Belkin and Heinemann, 1975, 1976; Heinemann and Belkin, 1977a, 1976b; Panday, 1975) can be explained as incidental as McGowan (1974:498) observed adult females of C. anomalus and C. ceratopogones (Theobald), species restricted to permanent waters in Africa, laying eggs in dishes of water in which the larvae undoubtedly would not survive.

Records of larvae of temperate Chaoborus species from temporary waters are likely from either a single generation of a multivoltine population which overwintered elsewhere in permanent waters, a population which eventually became extinct (see pg. 158) or are larvae which were transferred from over-flowing ponds upstream on a river to downstream inundation pools. Merely the presence of Chaoborus larvae in an aquatic habitat is not sufficient evidence to suppose survival of the population in this habitat. Records of C. americanus and C. flavicans fourth instar larvae from the Red Deer River near Innisfail, Alberta, when the river still had ice on its edge, showed all specimens with empty guts, suggestive of their inability to successfully survive to adulthood in this habitat. These larvae probably were washed into this permanent river from ponds further upstream. Records of Chaoborus larvae from the Hudson River, New York (Beck et al., 1975) are undoubtedly larvae from impoundments further upstream. Peus's (1934) often cited record of C. flavicans

from inundation pools along rivers in Germany and Reisen's (1973) observation of a single specimen of C. punctipennis from an inundation pool near a river in Oklahoma are therefore probably from larvae washed downstream from flooded ponds. Retreat of an over-flowing river in inundation areas can leave intact a population of Chaoborus larvae (Heinemann and Belkin, 1977a:272, see pg. 154).

5.1.1 Chaoborus trivittatus

Fedorenko and Swift (1972) found a population of C. trivittatus in an oligotrophic lake in southwestern British Columbia to be composed of two overlapping generations. Fourth instar larvae overwintered for two consecutive winters before pupating. Although adults emerged every spring, larvae which had overwintered only one winter did not pupate. Continual presence of fourth instar larvae throughout and after the pupal emergence period is therefore indicative of this two year life cycle.

I studied the life cycle of C. trivittatus from a pond 2.4 km. west of Edmonton which measured approximately 18 by 85 m., had a maximum depth of about two to three m. and was densely shaded by mature stands of Populus balsamifera and Picea mariana. Sampling during 1975 (Table 50) produced few fourth instar larvae on May 13, all of which pupated by May 26. Those data evidence a univoltine population of C. trivittatus. Changes in pupal and pupal exuvial sex ratio is explained by earlier pupation of male larvae (Table 51) and less time for development of male pupae (pg. 175). Emergence of adults was restricted to those few weeks in May. Eggs hatched in three to four days under laboratory conditions.

Table 50. Number of C. trivittatus immatures collected 2.4 km. west of Edmonton, Alberta.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
26-IV-1975				234				
8-V-1975				5	218	156		
13-V-1975				2	186	274	195	134
26-V-1975	106	11	40			3		1
12-VI-1975	25	22	144					
13-VIII-1975				72				

Table 51. Numbers of pupae resulting from 45 individually reared fourth instar larvae of Chaoborus trivittatus collected 2.4 km. west of Edmonton, Alberta, 26-IV-1975.

Date	Male	Female
28-IV	18	4
29-IV	5	14
30-IV		3
4-V		1
Total	23	22

Overwintering of fourth instar larvae as a feature of C. trivittatus is reflected in the range of collection dates of material examined (Fig. 25B). Gaps in the record undoubtedly reflect lack of collected material (Fedorenko and Swift, 1972; Main, 1953). James and Smith (1958) also observed overwintering of some C. trivittatus larvae (as C. nyblaei).

Parma (1971b) has discussed how univoltine or multivoltine Chaoborus populations are a result of environmental factors and vary in response to type of habitat and geographical area. These observations explain the differences between the bivoltine life cycle of C. trivittatus described by Fedorenko and Swift (1972) and the univoltine life cycle described here. In addition, temporal bimodality of records of field collected adults in southern Ontario and Quebec and north-eastern United States (Table 52) suggest that some populations of the species are multivoltine in this region (see Balvay, 1977c; Hirvenoja, 1960, 1965; Parma, 1971b).

5.1.2 Chaoborus cooki

The only previous allusion to the life cycle of C. cooki has been by James and Smith (1958) who mention that some of the populations of C. nyblaei (probably = C. trivittatus and C. cooki) at Churchill, Manitoba overwintered as eggs.

The life cycle of C. cooki was studied from three locations. A pond 1.6 km. south of Jasper measured 10 by 41 m. and had a maximum depth of 0.9 m. during most of its existence. Shading on the north, south and west sides of the pond was provided by Salix and Picea mariana. The pond was located about 40 m. from the south bank of the Miette River

Table 52. Records of Field Collected Adult C. trivittatus from Southern Ontario and Quebec and Northeastern United States. Roman Numerals represent months and Arabic Numerals are: 1 = Days 1-10; 2 = Days 11-20; 3 = Days 21-30(31).

	1-IV	2-IV	3-IV	1-V	2-V	3-V	1-VI	2-VI	3-VI	1-VII	2-VII	3-VII	1-VIII	2-VIII	3-VIII	1-IX	2-XI	3-XI
North Burgess Twp., Ont.					X													
Black Lk., Ont.			X															
Cordova Mines, Ont.																X		
Lac de Jean Venne, P.Q.		X			X	X												
Old Chelsea, P.Q.																	X	
Worcester, Mass.			X															
Hampton, N.H.			X						X									
Elizabethtown, N.Y.								X	X						X			
Bear Mountain, N.Y.																		X

and although it did not initially receive its water from the river, I observed overflow of its banks and flooding of the pond to about six times its normal surface area on two occasions, on 19-VI-1976 and 30-VI-1976. Retreat of the river from this inundation zone seemed to leave most of the population of C. cooki intact. However, I did collect several larvae stranded in isolated pools which drained within one day after retreat of the river. This pond was dry by October 10, 1976.

A pond 32 km. west of Edson measured 11 by 29 m. and had a maximal depth of 0.7 m. during most of its existence and was well shaded by dense brush and trees of Picea mariana and Populus tremuloides. The pond was dry by November 11, 1976.

A third pond, 1.4 km. west of George Lake, measured 15 by 19 m. and had a maximum depth of 0.9 m. during most of its existence. Although surrounded by dense brush and trees of Picea mariana and Populus tremuloides on its north, east and west sides the pond was often in direct sunlight. However, larvae were almost always situated in the shade of numerous Typha. The pond dried up on two occasions, 23-VII-1976 and 30-X-1976.

Tables 53, 54 and 55 give, respectively, numbers of animals collected from these three sites. A common type of life cycle is apparent. There is a progression within one growing season, of first through fourth larval instars, pupation, and, observed at 1.4 km. west of George Lake and 1.6 km. south of Jasper, emergence of adults. Lack of records of larvae after the pupal period until the next spring suggests that C. cooki overwinter in these temporary aquatic habitats as eggs. This conclusion is supported by observed diapause of

Table 53. Numbers of C. cooki immatures collected 1.6 km. south of Jasper, Alberta. # symbolizes dry conditions.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
20-V-1975		3	27					
4-VI-1975			2	34				
17-VI-1975			1	33	20	1		
*13-VII-1975								1
25-IV-1976	93	7						
18-V-1976		10	48					
31-V-1976			53	20				
13-VI-1976			2	18				
30-VI-1976				14	5			
*9-IX-1976								
8-X-1976	##########							
28-IV-1977	91	32						
12-VII-1977				31	7	3		

*C. americanus larvae present.

Table 54. Numbers of C. cooki immatures collected 32 km. west of Edson, Alberta. # symbolizes dry conditions.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
3-VI-1975	1		26	31	1			
17-VI-1975				4	1			
27-IV-1976	8	11						
18-V-1976		2	16	7				
29-V-1976		1	5	3	1	3		
9-IX-1976								
8-X-1976	##########	##########	##########	##########	##########	##########	##########	##########
11-XI-1976	##########	##########	##########	##########	##########	##########	##########	##########
1-I-1977	##########	##########	##########	##########	##########	##########	##########	##########
27-IV-1977		1						
*8-VII-1977								
*29-VII-1977								

*C. americanus larvae present.

Table 55. Numbers of C. cooki immatures collected 1.4 km. west of George Lake, Alberta. # symbolizes dry conditions.

DATE	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
	1	2	3	4	Male	Female	Male	Female
12-V-1975			18	20				
24-IV-1976		12	8					
6-V-1976		1	19	29				
13-V-1976		1	2	57	1			
25-V-1976				21	6	8		
23-VII-1976	##########							
*18-IX-1976								
30-X-1976	##########							

*7 C. trivittatus and 1 C. americanus Fourth instar larvae collected.

C. cooki eggs in the laboratory and their resistance to desiccation (pg. 170). However, in spite of this adaptation to temporary waters, C. cooki larvae may occasionally live in permanent ponds (e.g. 2.4 km. west of Edmonton).

This univoltine life cycle in which the eggs overwinter is reflected in the restricted temporal distribution of records of fourth instar larvae of C. cooki (Fig. 25B).

It is clear that this species circumvents the problems presented by temporary habitats to other Chaoborus species. Larvae of C. americanus were collected from each of the three sites studied late in the season (Table 53, 54, 55) and these undoubtedly died when the ponds became dry. Both live and dead C. trivittatus larvae and a live C. americanus fourth instar larva were picked up off wet mud at the location 1.4 km. west of George Lake on 18-IX-1976.

The unique life cycle of C. cooki in temporary ponds allows this species to avoid competition with other sympatric Chaoborus species except when some of these occasionally inhabit the same temporary ponds. Even so, these would be as younger instars than those of C. cooki.

5.1.3 Chaoborus nyblaei

There is no direct evidence of the type of life cycle of C. nyblaei. However, a thick exochorion, similar to that of C. cooki would suggest that the egg is similarly adapted to resist desiccation and that this species also overwinters as eggs. C. nyblaei larvae have been collected from both a large permanent pond and a small pool a few meters in diameter in northern Fennoscandia (Hirvenoja, 1961).

Low number of eggs per female would support the conclusion that C. nyblaei immatures inhabit temporary ponds (see pg. 139). Collection of adults only in the later part of July agrees with this interpretation of the type of life cycle.

5.2 Development and Behavior

5.2.1 Adults

Parma (1971b:45) described the emergence of adult C. flavicans and C. crystallinus. Most observations of C. trivittatus and C. cooki concur with that description but the following are additions or differences. Wings are released from the exuviae after the antennae but before the legs become free. Each of the forelegs and midlegs are released one after the other but the hindlegs are pulled out together. While the hindlegs are becoming free the wings are folded over the abdomen. Emergence, from the time of the dorsal split to complete release from the exuviae is, under laboratory conditions, 44-95 seconds (n=28) for male and 47-92 seconds (n=25) for female C. trivittatus and 39-70 seconds (n=30) for male and 38-51 seconds (n=13) for female C. cooki. All adult C. trivittatus emergences in the laboratory occurred during daylight conditions and those of C. cooki only took place during night-time hours. Myconial fluid is released in 5-21 drops. Males and females of both species flew readily after release of at least some of the myconial fluid but while females flew only a short distance before landing again males would fly much longer distances. At 20°C both C. trivittatus and C. cooki males completed rotation of their genitalia within four hours.

Males of both species possess at least some mature sperm upon emergence. Differences in ovarial development between teneral females of C. trivittatus and C. cooki are described elsewhere (pg. 138).

Chaoboridae are commonly designated as non-biting mosquitoes. However, Cook (1956:6) states that 'Chaoborinae (=Chaoboridae) have all structures necessary for piercing and for feeding on fluids'. Felt (1904), Pucat (1965) and Theobald (1901a:62) suggested that adult Chaoboridae feed on plants but these claims were unsubstantiated by data. Martini (1931) also recognized adults to be capable of feeding but gave no actual observations.

Both mammalian and avian blood have been found in the guts of female Corethrella brakeleyi (Coquillett) and Co. wirthi Stone (Williams and Edman, 1968). Miyagi (1974) reported the presence of a blood meal of unknown origin in the gut of a female Co. japonica Miyagi. Its mandibles and hypopharynx are serrated as are those of female Co. brakeleyi, Co. wirthi and Co. appendiculata Grabham (Miyagi, 1975).

Jenkins and Knight (1950) reported an adult male Eucorethra underwoodi probing or feeding at pistillate flowers of willow.

Adult Mochlonyx cinctipes (Coquillett) did not feed on proffered prunes, raisins, honey-water or wild flowers, although imbibition of water was observed in the field (O'Connor, 1959). M. velutinus (Ruthe) took diluted honey (James, 1957).

Some workers have reported on adult life span of chaoborids but most, unfortunately do not report their experimental conditions (Table 56).

While collecting adult C. trivittatus 2.4 km. west of Edmonton, Alberta on May 13, 1975 I observed that male and female adults often alighted on the pond surface and applied their mouthparts to the water for about 30 seconds, rested for a short period and then flew away. Air temperature was 17°C. In addition, two males alighted on the ground

Table 56. Life span of chaoborid species previously reported.

Species	Life Span (in days)	Author
Eucorethra underwoodi	15	McCloy (1950)
Mochlonyx velutinus	10	McCloy (1950)
M. cinctipes	12-14	O'Connor (1959)
Chaoborus crystallinus	1-3	Parma (1971b)
	1-3	Sikorowa (1973)
C. flavicans	1.5-6	Parma (1971b)
	8-14	Wesenberg-Lund (1919)
	1-4	Sikorowa (1973)
C. anomalus	2-3	McGowan (1974)
	1-5	Verbeke (1957)
C. ceratopogones ♀	2-3	McGowan (1975)
C. edulis ♂	1-2	McGowan (1975)
C. edulis ♀	3-6	McGowan (1975)
C. obscuripes	21	Wesenberg-Lund (1914)
	1-3	Sikorowa (1973)
C. astictopus	1-5	Lindquist and Deonier (1942b)
C. punctipennis	3-5	Muttkowski (1918)
	3-5	Juday (1921)
C. pallidus	1-5	Sikorowa (1973)

and walked with their front legs moving alternately in sweeping motion similar to that described by Downes (1974) for adult chironomids searching for honeydew. At this time of year no aphids were present to provide this source of nutrition. Adults commonly exhibit this searching behavior under laboratory conditions if kept in sealed mason jars for at least 24 hours without water.

These observations led me to suspect that adults drink water and that this may be an important factor in prolonging adult life span and consequently influence adult dispersal capabilities.

I carried out a feeding experiment to see if adults drink water and to determine if water uptake affects longevity.

Blue excreta in jars supplied with dyed water showed that both males and females imbibe water. Longevity results are shown in figures 35A,B. These results were compared statistically using a Duncan's Multiple Range test ($p<0.05$) and it was found that: 1) there is no significant difference in longevity between males or females given either clear or dyed water, 2) males which could not drink lived for a significantly shorter period than males which could drink water, 3) females which could not drink lived for a significantly shorter period than females with dyed water and 4) although there was no significant difference between females without access to water and those with clear water, this is explained by the low numbers in each treatment; comparison of females without access to water to combined results of females with dyed or undyed water available using a T-test revealed them to be significantly different at the 98% level.

These results show that C. trivittatus adults can imbibe water and that this significantly increases their life span. Longevity of

adults of most other species may have been seriously underestimated.

During the springs of 1974-1977 I made daytime observations of behavior of C. trivittatus adults 2.4 km. west of Edmonton, and 16 km. west of Jasper, Alberta. Males were more often seen throughout the emergence periods. They formed columnar swarms of 1-132 (n=8) individuals at the periphery of ponds at heights of about 0.3-1.8 m.. Females were sedentary on surrounding vegetation, particularly on tree trunks. When disturbed they flew and were easily seen. However, on May 13, 1975, after 1.5 hours of collecting with an aspirator and aerial net from tree trunks and low vegetation at 2.4 km. west of Edmonton, only 32 females were procured. Concurrently, males in swarms were extremely numerous. Similarly, 25 females and 218 males were collected with an aspirator from tree trunks at this locality May 7, 1977. Female pupae and exuviae composed 59.6% (n=460) and 40.7% (n=329) of a sample respectively, collected May 13, 1975. The possibility that the over-abundance of males was due to their earlier emergence as might be suggested from lab rearings, is therefore unlikely.

When females made one of their occasional flights through a male swarm, they were invariably seized front to front by a male. The pair interlocked genitalia and fell immediately to the ground where they assumed an end to end position. Matings lasted 51-64 seconds (x=58.7, n=5). Nine other matings observed required a similar period of time but were not measured exactly.

These data suggest the following pattern. Most adult males emerge earlier than females and form large swarms at the periphery of the ponds from which they emerged. Females, after emergence and an unknown period of time, fly through this 'barrier' of males and

are mated. Because the sex ratio of emerging adults is nearly 1:1 (Table 51), the far greater proportion of male adults at pond peripheries suggests that females are the main dispersing agent of this species. Well developed ovaries at emergence are probably correlated to the stable habitat which this species inhabits and suggests that C. trivittatus female adults cannot disperse as great distances with their fully developed eggs as can C. cooki female adults (see below).

If a sex ratio of nearly 1:1 and observations of concentrated male swarms at the periphery of water bodies alone are indicative of this type of adult behavior (i.e. females mated at the pond or lake periphery and subsequently dispersing), observations of adults of the species of Chaoborus s. str. suggest that these exhibit similar behavior. Bradshaw (1973) reported males to compose 57% of populations of C. americanus. I have observed large male swarms of this species at the periphery of numerous ponds near Edmonton, Alberta. Males make up 43-45% of C. flavicans populations (Parma, 1971b) and swarms have been observed at a number of localities (Berg, 1937). Parma (1971b) noted the concentration of male C. flavicans at the periphery of the water bodies he studied. Parma (1971b) reported males to comprise 39-60% of C. crystallinus populations and both he and Nielsen and Greve (1950) have observed male swarms of this species. Neither sex ratio or swarming behavior have been recorded for C. obscuripes (van der Wulp). These data suggest that at least three of the four species of Chaoborus s. str. share a common type of adult reproductive behavior and dispersal with C. trivittatus. The

significance of this is discussed in the section on zoogeography and speciation.

I have little data on adult behavior of C. cooki in the field. In 1975 and 1976 at the pond 1.4 km. west of George Lake and in 1976 at the pond 1.6 km. south of Jasper, Alberta, emergence of adult C. cooki was observed only during the night. Although both New Jersey and CDC light traps were present at the edges of the ponds, adults that emerged were not trapped. Upon emergence, adults flew upward out of the field of vision. On the day after each of the nights I observed emergence, I swept with an aerial net all surrounding vegetation for at least 100 m. in each of a north, south, east and west direction of both ponds but with no captures. I also visually examined the immediate area and climbed the trees surrounding the ponds but neither collected nor saw any adults.

Timing of laboratory matings of C. trivittatus adults (45-65 seconds, n=6) approximated those observed in the field (see above). This would suggest that timings of matings of C. cooki adults in the laboratory (91-122 seconds, n=8) also approximates those under field conditions.

These data, a sex ratio of males to females of about 3-5 to 1 (see pg. 175), and retarded ovarial development indicate that C. cooki adult behavior differs substantially from that of C. trivittatus. This suggests that C. cooki adults do not remain near the pond from which they emerge and both males and females disperse. This behavior would ensure the survival of at least part of the total population. Temporary ponds which became dry before adult emergence would undoubtedly kill the immatures present.

Female adults probably exhibit underdeveloped ovaries on emergence so that fat body can be used as energy for flight should a suitable habitat not be located and would guarantee at least the production of a few eggs once a suitable habitat is found (Roff, 1977).

Lack of records of adults in the area from which they just emerged suggests that the adults mate after at least a period of dispersal. Greater percentages of males than females would be more conducive to successful mating after dispersal and explains the inequality in numbers of males and females.

Differences in dispersal capabilities and behavior of C. trivittatus and C. cooki concurs with the suggestion by Southwood (1962) that generally species found in unstable habitats show more intensive dispersal behavior than do those in more stable habitats. For species of Chaoborus, degree of ovarial development in teneral adults (Fedorenko, 1975c; Parma, 1971b) and number of eggs per female (Fedorenko, 1975c; McGowan, 1974; Parma, 1971b; Sikorowa, 1973) is also correlated to stability of habitat.

Egg rafts of C. trivittatus are laid in a similar way to those of C. flavicans and C. crystallinus (Parma, 1971b:28). I did not measure the rate of egg laying. I have observed oviposition in the field during daylight hours.

I have no observations of oviposition by female C. cooki.

5.2.2 Eggs

Egg rafts of C. trivittatus, like those of species of Chaoborus s. str. (McCloy, 1950 (as C. crystallinus = C. americanus); Parma, 1971b; Sikorowa, 1973) are in the form of floating discs with the eggs arranged in a spiral. Observations of egg rafts and egg development are similar to those reported by Parma (1971b:30). I found many egg rafts stuck to floating debris at the water surface. Eggs in the laboratory turn dark brown after one or two days. The pharate first instar larvae were positioned as shown by Parma (1971b: fig. 12) for C. flavicans. As Parma (1971b:29) has pointed out, oviposition can be disrupted and I therefore did not consider number of eggs per raft to be a significant measurement. I have found an egg mass, for example, of C. trivittatus composed of nine eggs. This clearly does not reflect the number of eggs per female (pg. 138) as implied by Parma (1971b:30) and therefore cannot be used to interpret interspecific or intraspecific variation.

Eggs of C. cooki were obtained only from laboratory mated females. These were laid in a semispherical mass on the walls of vials, which were used to retain adults. The eggs were held together with minute amounts of gelatinous matrix. The exochorion of each individual was also sticky. Endochorions of fertilized eggs turned dark brown within two to three days. Non-fertilized eggs turned slightly brown in patches of the endochorion.

I attempted to collect eggs of C. cooki from the site 1.4 km west of George Lake, after the pond had become dry on October 30, 1976

when the surface soil was frozen to a depth of about one to three cm.. Soil samples were taken from each of 50 by 50 cm. grids on the entire area covered by the high water mark of the temporary pond. When Typha stems were present in a grid a sample was taken of these cut off from below the soil surface. In addition, samples of brush that immediately surrounded the pond were taken. In the laboratory soil samples were sieved and vegetation scanned under the binocular microscope. Nine soil samples were treated with floatation techniques using NaCl. I was unable to retreive any eggs or egg shells.

I have observed hatching of eggs only for C. trivittatus from 2.4 km. west of Edmonton and 16 km. west of Jasper, Alberta. The events of hatching were similar to those described by Parma (1971b:32). Eggs of C. trivittatus hatch within three days, usually all of one egg mass hatching within a few hours. A few eggs were sieved from a bottom sample taken from a pond 16 km. west of Jasper, Alberta on June 18, 1976 after the adult emergence period was completed. All eggs were white suggesting they were not fertilized and by June 24, 1976, all had deteriorated in the laboratory. Outer eggs on the egg raft hatch first. Eggs of C. trivittatus split longitudinally and the posterior part of the larvae are freed. A few were caught with their head capsule stuck in the egg shell but most, with violent struggling, freed themselves. Unlike the egg shells of C. crystallinus and C. flavicans (Parma, 1971b: fig. 13), and C. americanus (pers. obs.) which the egg shell on each side of the longitudinal slit folds inwards, the sides of the egg shell of C. trivittatus fold outward (Fig. 9D). This unique character may have evolved to compensate for the large size of C. trivittatus first instar larvae and therefore

allow for fewer numbers of first instar larvae being stuck in the egg shell.

All eggs of C. trivittatus collapsed under atmospheric conditions and therefore are not resistant to desiccation.

Eggs of C. cooki do not hatch within a few days as do those of other Chaoborus species (Deonier, 1943; Herms, 1937; McGowan, 1974:498; Sikorowa, 1973:76). Endochorions of these eggs, white when laid, become extremely dark brown within 2-3 days. Larvae develop to at least a stage where head capsules and air sacs are visible but do not hatch under temperatures of 20°C. After three months at this temperature and an 18:6 L:D photoperiod, some eggs were treated with either three successive floodings, three days apart, of deoxygenated water or one treatment with xylene vapor but failed to hatch. Other eggs were treated to 20°C temperatures and 18:6 L:D photoperiod for two months, 2°C and total darkness for four months and returned to former conditions with no evidence of hatching. A few eggs did not hatch after being kept at 20°C and 18:6 L:D photoperiod for two months and then total darkness at 2°C for ten months. Study of the egg shell showed that the exochorion was gone (as it was in some unhatched eggs) and the chorion had split to release the larva in a way different (Fig. 9E) from those described for other species.

Eggs of C. cooki were treated to one month of atmospheric conditions without collapse. The thick exochorion is apparently a protective layer against desiccation. The highly sculptured exochorion, furthermore, probably functions as a plastron under alternately dry and wet conditions (Hinton, 1969; Hinton and Service, 1969).

5.2.3 Larvae

I observed horizontal clumping of second, third and fourth instar larvae in ponds which were not entirely shaded from direct sunlight. Clumping was related to presence of shade provided either by surrounding vegetation, topographical features, or emergent aquatic vegetation. This is clearly a factor which influences sampling results of C. trivittatus and C. cooki larvae from shallow water bodies. For example, a pond measuring about 5 by 14 m., 7.6 km. northwest of Mountain Park, Alberta was sampled successively with a dip net along the north side and a portion of the south side which were exposed to direct sunlight, without collecting a single larva. A prominent boulder on the south shore provided shade in part of the pond and in this region I collected 109 fourth instar larvae of C. trivittatus in a single sweep of the net.

Similar reponse to shade is probably exhibited by C. pallidus (Edwards, 1920; Sikorowa, 1964; Akehurst, 1922:352).

This factor is probably one which influences the restriction of Schadonophasma species to woodland conditions. In addition, it is possible that this response to shading is a modification of the response to light which is important in vertical migration of some species (Chaston, 1969; LaRow, 1968, 1969).

I observed grooming behavior of fourth instar larvae of C. trivittatus and C. cooki. Larvae often lashed at the posterior portions of their bodies with their antennae and mandibles. Occasionally larvae place the posterior portion of the abdomen in

their oral cavity, the anal fan being completely in the mouth. Even the slightest disturbance results in restoration of a normal position. However, on one occasion I observed a larva of C. trivittatus keep its tail end in its mouth for over 2.5 hours. This behavior is undoubtedly an important adaptation for removal of epibionts.

I did not observe larvae of C. trivittatus or C. cooki bury themselves in the bottom substrate in aquaria, although when disturbed they would dart toward the bottom and often cling with mouthparts to bottom debris.

Although differences in prey type were evident between C. trivittatus and C. cooki, I did not quantify this information because of biases produced by preservation techniques (Swift and Fedorenko, 1973). Although Fedorenko (1975a, 1975b) and Swift and Fedorenko (1975) have recorded the diet of C. trivittatus fourth instar larvae from an oligotrophic lake in southwestern British Columbia as composed of copepods and cladocerans, it is not known to what extent change of habitat, such as a pond, affects prey type. For example, I observed C. trivittatus fourth instar larvae capturing chironomid larvae 2.4 km. west of Edmonton, Alberta. I did not find ostracod remains in the gut of C. trivittatus fourth instar larvae and in the lab they lashed out at but rejected ostracods as food. Contrary to this I found numerous C. cooki larvae with ostracods in their crops. Chironomid and, in C. cooki larvae from some ponds, culicid larvae were also common. To a certain degree differences of prey type must reflect habitat differences but these observations of ostracod ingestion suggest species differences in ability to ingest at least this prey type.

Male larvae of both species pupate earlier than do female larvae (Table 51, 57). C. cooki larvae have a more extended pupation period than do those of C. trivittatus.

Table 57. Numbers of pupae resulting from 42 individually reared fourth instar larvae of C. cooki collected 32 km. west of Edson, Alberta. Pupation recorded only on dates presented.

Date	No. of Pupae	
	Male	Female
5-VI-1975	0	0
6-VI-1975	4	0
9-VI-1975	25	2
13-VI-1975	2	7
16-VI-1975	1	0
20-VI-1975	1	0
Total	33	9

5.2.4 Pupae

Pupation of Chaoborus has not previously been observed. The following is a compilation of a single pupation observed for each of C. trivittatus and C. cooki. Under laboratory conditions pupation required about two or three seconds. The fourth instar larva suddenly contracted along its entire body length in a quivering motion. The larva turned into a vertical position, the pupal horns popped through the thoracic suture, followed by the thorax and head of the pupa. The larval exuviae slipped down the length of the pupal abdomen and was thrown off the tip by a forward flick of the abdomen.

Parma's (1971b:38) description of macroscopic color changes during pupal development also apply to pupae of C. trivittatus and C. cooki.

The pupal period under laboratory conditions of C. trivittatus is three (n=1) to four days (n=85) for males and four (n=22) to five (n=4) days for females. The pupal period of male C. cooki lasted two to six days (n=1,2,6,28,21 respectively) and of females three to seven days (n=1,13,13,11,4 respectively).

Differences of development of ovaries between pupae of C. trivittatus, C. cooki and C. nyblaei are described elsewhere (pg. 138).

To compare the sex ratio of C. trivittatus and C. cooki I collected fourth instar larvae before any indication of pupation in the field, from 2.4 km. west of Edmonton and 32 km. west of Edson, Alberta (not the same locality from which the life cycle of C. cooki was studied), respectively. Individual rearings of 44 larvae of C. trivittatus produced 23 male and 21 female pupae and 42 C. cooki larvae

produced 33 male and nine female pupae. The use of a compound character index to sex fourth instar larvae of C. cooki (pg. 103) from 1.6 km. south of Jasper indicated a sex ratio of 52 males to 10 females.

6. Mating Experiments

Observations of forced matings in the laboratory between members of two populations give indications of their reproductive compatability and therefore their conspecificity. I tested my interpretation of morphological, bionomic and temporal discontinuities as indicative of the presence of two species of Schadonophasma in North America by attempting to cross individuals of C. trivittatus and C. cooki.

Results of crossing (Table 58) show several important features. Reduced number of eggs and of these, number of fertilized eggs, of crossings of male C. trivittatus and female C. cooki as compared to intraspecific crossings showed a reduced fertility. Four of the six crosses resulted in no eggs being laid. Reduced fertility and low number of eggs from some of the intraspecific crosses must be the result of experimental conditions.

Crosses between male C. cooki and female C. trivittatus resulted in no eggs. It was apparent during the crossings that male C. cooki had difficulty in latching onto the female genitalia. In an additional six attempted couplings the penis valves of male C. cooki could not insert into the female genitalia of C. trivittatus and copulation did not take place. This may be due to the more bulbous nature of the head of penis valves of C. cooki which cannot fit into

Table 58. Results of Intraspecific and Interspecific Crossings of Adult C. trivittatus and C. cooki.

Species crosses (♂ X ♀)	Specimen No.	No. of Eggs	% Fertile
TRIV. X TRIV.	1	190	98.4
	2	133	71.3
	3	27	77.8
	4	180	60.0
	5	171	97.1
COOKI X COOKI	1	78	61.5
	2	72	86.1
	3	73	88.7
	4	70	70.4
	5	0	0
COOKI X TRIV.	1	0	0
	2	0	0
	3	0	0
TRIV. X COOKI	1	85	11.8
	2	65	0
	3	0	0
	4	0	0
	5	0	0
	6	0	0

the proper receptacle in the female genitalia.

These observations indicate reproductive isolation between C. trivittatus and C. cooki is additionally maintained by mechanical and genetic incompatibilities.

7. Phylogeny and Zoogeography

Phylogenetic and zoogeographic considerations are logical conclusions to systematic studies. In this section I give my working principles for such considerations, evidence for the recognition of three species of Schadonophasma and hypothesize their evolutionary history. Because the evolution of species of Schadonophasma can be best understood in the context of ex-group comparisons I also consider the evolution of the genus Chaoborus.

In recent years there has been much debate concerning the principles and methods of cladistic analysis as used to infer phyletic relationships (e.g. Ashlock, 1974; Brundin, 1972; Darlington, 1970; Griffiths, 1972, 1974; Hull, 1970; Mayr, 1974; Schlee, 1975; Sneath and Sokal, 1973; Sokal, 1975; and papers cited in these). Although adherance to methods themselves can blind investigators to more reasonable alternative interpretations (Darlington, 1970), it seems likely to me that Hennigian principles (see Kavanaugh, 1972) have broad applicability in the determination of evolutionary relationships. I have therefore used them to infer the evolutionary history of species of the genus Chaoborus.

One potential source of error in the application of cladistic analysis concerns the weighting of characters on a superficial basis. Hecht and Edwards (1977) and Szalay (1977) have discussed the importance of detailed investigation of individual characters used in phylogenetic analysis. Although this may not be possible in many studies, this

investigation provided a basis from which to better interpret the evolutionary significance of most characters used and therefore improved the use of cladistic techniques. These data allowed a more probable interpretation of the evolution of some Chaoborus species and in particular, of the species of Schadonophasma.

Most systematic studies, some because of a lack of bionomic information, only consider allopatric speciation as the means of evolution of lineages. In a recent study Tauber and Tauber (1977) have proposed a genetic model for sympatric speciation of more general applicability than that proposed by Bush (1975a, 1975b). However, most studies suggesting interpretations of sympatric speciation lack study of the phyletic relationships between the organisms concerned. My interpretation of possible speciation events in the history of Schadonophasma species provides an example of how phyletic relationships and zoogeographical considerations may give supportive criteria for inferring an allopatric or sympatric speciation model.

Darlington (1970:3) has criticized assumptions of dichotomous speciation and describes several situations in which branching was possibly polychotomous. I have not found evidence of trichotomous speciation of the three species of Schadonophasma. The presence of synapomorphies for two of the species supports only dichotomous speciation in the history of Schadonophasma species.

7.1 Evidence and Recognition of Three Species of Schadonophasma

The basic taxonomic unit used for inference of phylogenies is the species or species group. A phylogeny therefore depends on correct interpretation of the diversity it attempts to explain. The following is a discussion of evidence for the recognition of three species of Schadonophasma.

Morphological, bionomic, developmental and behavioural incongruities as well as differences in geographic variation and distribution among groups of populations are logical criteria for recognition of species if the biological species concept is accepted as a testable hypothesis. Only experimental tests of reproductive incompatibilities, however, might provide direct evidence of reproductive isolation. It is the concordance of such indirect and direct evidence of reproductive isolation that allows systematists to interpret the former as the result of such reproductive isolation. The results of this study, as many others, confirm the validity of this assumption.

From the results of this study I consider discontinuities in the following features to support my conclusion that there are two species of Schadonophasma in North America recognizable as C. trivittatus and C. cooki.

1. Structure of eggs, all stages of larvae, pupae and adults.
2. Pattern of development of LB/AL from first through fourth instar larvae.
3. Characters of fourth instar larvae which are sex-associated in one species but not the other.

4. Correlations of characters of fourth instar larvae.
5. Patterns of geographical variation of characters of fourth instar larvae in Alberta.
6. Rates of development of eggs, larvae and ovaries of adults.
7. Life cycle and types of habitat commonly occupied.
8. Larval prey type.
9. Adult behavior.
10. Reproductive compatibilities when adults from different populations were crossed in the laboratory.
11. Lack of sympatry in western and eastern coastal regions of the United States.

I do not have nearly the same amount of evidence to justify recognition of the third species C. nyblaei in Fennoscandia. Because of similarity of compared semaphoronts, I assumed that all specimens from Fennoscandia were conspecific. Adult material collected 2-3 km. SW of Nuorgam, Finland, on July 24, 1960 was probably conspecific with larval and pupal material collected there.

Most characters of the immatures and color of adults of C. nyblaei are similar to those of C. cooki. However, shape of the adult male penis valve and prelabral appendage of fourth instar larvae are most similar to those of C. trivittatus. This combination of features suggests the presence of a third species and this is further supported by extremes of variation of certain characters of the fourth instar larvae of C. nyblaei (number of mandibular fan bristles and anal fan setae).

Because of the difficulties of interpretation of morphologically similar, allopatric populations separated by a geographical area from which specimens are not known (Mayr, 1969), it is impossible to be certain that C. nyblaei is a separate species. Therefore it might

be conspecific with either C. trivittatus or C. cooki. Overall morphological similarity would indicate, if this were so, that C. nyblaei and C. cooki are conspecific. However, patterns of geographical variation of C. cooki would not suggest that the higher mean values of number of anal fan setae and lower mean value of number of anal fan setae of the larvae of Schadonophasma in Fennoscandia are the result of variation of those characters of C. cooki. Nevertheless, the possibilities of character displacement producing such features as exhibited by the population in Fennoscandia cannot be presently negated. Further study of C. nyblaei populations to complement the data given in this study for C. trivittatus and C. cooki, further investigation of the range of C. nyblaei and detailed analysis of geographical variation of C. nyblaei and C. cooki once further samples become available, would give further clues to questions of conspecificity. At any rate, it is almost certain that the Bering Strait area is devoid of Schadonophasma populations and presents at least a recent barrier to North American and, should they exist, eastern Asian populations of Schadonophasma.

7.2 Phylogeny of *Chaoborus*

Saether (1970), using cladistic methods, proposed a phylogeny of *Chaoborus* species and chaoborid genera but dealt only with those of the Holarctic region. He used 29 characters to determine relationships among subgenera of *Chaoborus*. However, his interpretation of the polarity of many of these characters is questionable.

A number of characters are used by Saether (1970) for which he gives no criteria for determining the apomorphic and plesiomorphic ends of the morphoclines and for which there are none apparent (Maslin, 1952). For example, the character HW/WBE is considered plesiomorphic if 2.5-4.2 and apomorphic if 1.5-1.8. However, the closest sister group to *Chaoborus* for which these data are available is *Mochlonyx* which, if all species are considered, has a total range of 1.82-2.36 (Cook, 1956). If this feature represents the plesiomorphic condition of *Chaoborus* both ends of the morphocline recognized by Saether would be apomorphic. However, HW/WBE ratio of male adult *Eucorethra underwoodi* is 8.3-8.5 (Cook, 1956) and this may also reflect plesiomorphy. Until further ex-group comparison has been made, phylogenetic interpretation of this character is conjectural.

It is also not clear how Saether interpreted the polarity of morphoclines of values of Y/R_3 and Y/X of adults (males?), width/length of abdominal segment VII of pupae and AS/AL of larvae, when these data were available only for some species of *Chaoborus*.

It is well known that character states which involve loss of a feature are particularly suspect of convergent or parallel evolution (e.g. it could be as likely for species to independently

lose features as for a single ancestor of species to do so). Interpretation of the following characters states as synapomorphic provides at best an uncertain basis for reconstructing a phylogeny: loss of parascutellar setae and reduction of number of mesepimeral and pronotal setae of adults, loss of colour of the pupal paddle membrane, reduction of the relative length of the median rib of the pupal paddle and reduction of the larval tentorium.

Shape of the apex of the male adult dististyle and loss of a pair of larval labral setae are autapomorphies for C. pallidus and cannot be used to determine relationships between species or groups of species.

Saether (1970:47, Trend 46) considered the placement of the simple seta toward the apex of the median rib of the pupal paddle to be apomorphic within Chaoborus. This condition, however, most closely approximates the condition featured by Mochlonyx and Eucorethra pupae suggesting that it is more likely the plesiomorphic character state.

Following Saether's (1970) publication, larvae of some African species have been well described (Green and Young, 1976; McGowan, 1972, 1976). In addition, Saether (1976) has redescribed adults, pupae and fourth instar larvae of C. brasiliensis (Theobald) and C. magnificus Lane from Venezuela. Using these descriptions and my own observations I have constructed a phylogeny of those species of Chaoborus for which sufficient information is available. The characters used and interpretation of their plesiomorphic and apomorphic states are given in Table 59. All character states were judged plesiomorphic or apomorphic on the basis of ex-group comparisons (especially Mochlonyx

Table 59. Characters and character states within the genus Chaoborus.

Character	Plesiomorphic	Apomorphic
Adults		
1. Leg coloration	Pigmented only at bases and apices of leg segments and tarsal articles	Femur and tibia ringed or spotted along their lengths
2. Wing coloration	Spotted	Not spotted
3. Basistyle shape	No protuberance on inner face	Protuberance on inner face
4. Penis valve	No apical claw when head rounded	Apical claw and rounded head
5. Comb-like setae on 3rd tarsomere of female	Absent	Present
Pupae		
6. Median rib of pupal paddle	Straight at apex	Curved at apex
7. Median rib of pupal paddle	Extended to edge of paddle	Not extended to edge of paddle
8' Prelabral appendage	Setose; covered with spines	Broadened with spines directed anteriorly and posteriorly
8'' Prelabral appendage	Broad with spines directed anteriorly and posteriorly	Broad with spines directed only anteriorly
8''' Prelabral appendage	Broad with spines directed anteriorly and posteriorly	Setose but with spines directed only anteriorly and posteriorly
Larvae		
9. Antenna	Not curved at posterior base	Curved at posterior base
10. Dorsal Process	No article present	Single article present
11. Tentorium	Strongly sclerotized and thick	Weakly sclerotized and thin
12. Subordinate Mandibular Tooth	Not spinose	Spinose

and Eucorethra) with the exception of prelabral appendage shape. The interpretation of several characters requires special comment.

Two characters used are interpreted as apomorphic in their reduced state: relative length of the median rib of the pupal paddle and relative degree of sclerotization and size of the larval tentorium. These were used because of a shortage of characters in this analysis. As proposed here, reduction of the larval tentorium has occurred twice.

The prelabral appendage of Chaoborus larvae is undoubtedly a seta (Balvay, 1977c). Although which seta of other chaoborids is homologous to the prelabral appendage is not known, it is reasonable to assume that ontogenetic development of the prelabral appendage from a simple seta in the first two instars of all Chaoborus species to a laterally flattened appendage in the last two instars of some species corresponds to the evolution of these setae (Akehurst, 1922:352).

The only clue for determining the polarity of AS/AL of Chaoborus larvae is provided by the larvae of Eucorethra underwoodi. Mochlonyx larvae examined did not have an antennal seta. The AS/AL of three fourth instar larvae of Eucorethra underwoodi was 0.51-0.59 (mean = 0.558). If this states reflects the primitive condition, any ratio greater or less than this can be considered apomorphic. In the construction of the phylogeny I have used this feature only to interpret the extreme values of AS/AL of Schadonophasma as apomorphic. Change of this ratio from a low value in first instar larvae to a high ratio in fourth instars (Fig. 22A) would support such an interpretation.

The polarity of two characters, coloration of adult legs and state of the larval dorsal process, has apparently been misinterpreted by Saether (1970). He suggested that ringed legs of adults is a plesiomorphic state. This is probably only partially true. Although color of bases and apices of leg segments and articles are dark in a number of ex-groups and is therefore probably plesiomorphic, spotted legs of some African species of Chaoborus (Verbeke, 1958) and species of the subgenus Sayomyia (e.g. C. punctipennis, C. astictopus, C. brasiliensis) is probably apomorphic.

Saether (1970:50) also considered the two segmented dorsal process of the fourth instar larvae of some Chaoborus species to be the plesiomorphic condition for the genus and implies (Trend 67) that the dorsal process is actually the evolutionary vestige of the respiratory siphon. However, as pointed out by Cook (1956:14)'the annulation on which this "siphon vestige" occurs has a musculature which indicates that it is a segment. This then is segment 9, and the siphon occurs on segment 8. Thus, the term "siphon vestige" seems to be inaccurate'. In addition, Parma (1971a) followed the shape of the dorsal process from instar to instar of C. flavicans and found the pointed dorsal process to be present only in the later instars. If this feature represents the siphon vestige one would expect it also to be present in earlier instars. I further tested this hypothesis by examining the position of the tracheal trunks of fourth instar larvae of C. cooki. I found that thawing previously frozen larvae resulted in the trachea filling with gas, allowing them to be clearly observed. The tracheal trunks showed a notable dorsal bend in the eighth abdominal segment (Fig. 8D) similar to the dorsal

bend of the tracheal trunks of Mochlonyx larvae into the siphon (Montchadsky, 1953: fig. 1). Additional evidence which would suggest that the dorsal process is not part of the segment which carried the siphon concerns the position of developing pupal paddles of mature fourth instar larvae. Horsfall and Ronguillo (1970: fig. 5) show that the pupal paddles of Aedes stimulans develop within the respiratory siphon of the fourth instar larva. Observations of C. trivittatus and C. cooki larvae show the pupal paddles develop along the dorsal surface of only the eighth segment and not within the segment exhibiting the dorsal process.

These observations indicate that the small dorsal article of the ninth abdominal segment of larvae of some Chaoborus species is in fact a newly evolved feature and not the vestige of the respiratory siphon. Absence of such an article is therefore the plesiomorphic condition. The pointed dorsal process exhibited by C. flavicans and C. crystallinus fourth instar larvae is also probably an independently derived characteristic.

The most probable phylogeny of species of Chaoborus using the characters in Table 59 is presented in Figure 36. I accept Saether's (1970) conclusion concerning the phyletic relationships between the four species of Chaoborus sensu stricto. This phylogeny differs primarily from that hypothesized by Saether (1970, 1976) by considering C. albatus as possibly the sister species of C. magnificus and these species plus C. brasiliensis, C. punctipennis, and C. astictopus (hereafter designated as 'ambpa') the sister group of Schadonophasma plus Chaoborus s. str.. The placement of C. pallidipes is uncertain.

This species could equally well be the sister group of Schadonophasma plus Chaoborus s. str. or of the species group 'ambpa'.

The grouping of C. anomalus, C. ceratopogones and C. pallidus is tenuous. These are recognized as monophletic on the basis of leg coloration which, as here hypothesized, shows covergence with the species group C. brasiliensis, C. punctipennis, and C. astictopus. Any of C. anomalus, C. ceratopogones or C. pallidus could be considered a sister group of the species group 'ambpa' if the following events are assumed to have occurred: 1) the basal curvature of the larval antenna was secondarily lost in these species or the curvature evolved independently in species groups 'ambpa' and Schadonophasma plus Chaoborus s. str. and 2) C. albatus and C. magnificus secondarily lost the derived coloration of adult legs. However, these events provide a less parsimonious explanation than does the convergence of leg coloration as presented here. Similarly the development of a lobe on the inner face of the basistyle of both C. anomalus and the species group C. brasiliensis, C. punctipennis and C. astictopus is considered a result of convergent evolution.

A character which may be synapomorphous for C. anomalus, C. ceratopogones and C. pallidus, but for which observations were not available for all other species, is the basally swollen and highly curved postantennal filaments (Saether, 1970: fig. 6C). Verbeke (1958:43) also considered C. ceratopogones and C. pallidus to be closely related on the basis of similarity of adults, pupae and larvae.

Although the broadening of the prelabral appendage may have evolved independently four times, I here consider it to have occurred

only once. The setose appearance of the prelabral appendage of C. punctipennis and C. astictopus is therefore a derived state and is only superficially similar to the primitive condition. This explains why the setaceous prelabral appendages of these two species have spines directed only anteriorly and posteriorly.

7.3 Fossil Evidence

The study of fossils can give important evidence for the correct interpretation of the evolutionary history of a group of extant organisms. However, few systematists studying arthropods are fortunate to have such fossils available to them.

A number of authors have described or mentioned Chaoborus subfossils (Deevy, 1942; Frey, 1955, 1962; Goulden, 1966a, 1966b; Hofmann, 1971; Marland, 1967; Stahl, 1959, 1969) or fossils (Edwards, 1923; von Heyden, 1862; Hope, 1847; Meunier, 1904; Scudder 1890 (questionable identification); Serres, 1829). All of the fossil material is in need of redescription. I examined the fossil pupa and disarticulated pupal parts described by von Heyden (1862) as Culicites (= Chaoborus) tertiarius and am presently preparing a redescription of those fossils and of some larval fragments (mandibles and anal fans) also present on the brown paper coal. The pupal paddles exhibit median ribs which extend to the edge of the paddle and are curved apically. In addition, some of the larval mandibles have the subordinate tooth at the base of the two larger teeth, very similar to that of C. flavicans. It is not certain that the larval fragments are from the same species as the pupa and pupal parts. Nevertheless the mandibles would suggest that they are from a population conspecific with C. flavicans (Chaoborus s. str.) or from a species which is the sister species of C. flavicans. The apical curvature of the median rib of the pupal paddles is a synapomorphy grouping Schadonophasma and Chaoborus s. str.. Although I cannot confidently place the fossil

pupa or pupal parts with one of these lineages it is clear, if convergence has not taken place, that this species shares a common ancestry with or within either of these two subgenera.

Edwards (1923) has correctly recorded the age of the fossils as Upper Oligocene (Mägdefrau, 1968). This would indicate that the speciation giving rise to C. flavicans and its sister species C. crystallinus took place at least 25 million years B.P. and that therefore the speciation event which gave rise to the lineages represented by extant species of Schadonophasma and Chaoborus s. str. took place before that time.

The location of these fossils at Rott, Siebengebirge, West Germany is consistent with a hypothesis that the species group Schadonophasma plus Chaoborus s. str. evolved under temperate conditions. Sittler (1967) has discussed fossil assemblages with temperate elements from the Oligocene of Europe.

7.4 Phylogeny of Schadonophasma

Saether (1970) proposed a phylogeny for the species of Schadonophasma based on six characters. I have already discussed the difficulties of interpretation of four of these (number of mesepimeral and pronotal setae; ratio of Y/X; WS/LS; shape of dorsal process). Saether's interpretation of variation of the penis valve shape seems to be correct for Schadonophasma. The interpretation of body size variation is probably incorrect but is discussed below.

Although the phylogeny I propose for the species of Schadonophasma is identical to that by Saether (1970) except for his consideration of C. brunskilli (= C. trivittatus) as the sister species of C. trivittatus, my way of deducing this is substantially different. For the analysis I have chosen seven characters (Table 60), some of which are discussed below.

Saether (1970:43) in Trend 2, recognized the largest chaoborid, Eucorethra underwoodi to represent the plesiomorphic condition and the smallest size, the apomorphic condition. He therefore considers the large size of Schadonophasma species and within the subgenus, C. cooki and C. nyblaei, to be plesiomorphic. However determination of polarity of this morphocline is almost certainly incorrect. Schadonophasma species are the largest of all described Chaoborus species and are larger than all species of Cryophila Edwards, Mochlonyx, Promochlonyx Edwards, and Australomochlonyx Freeman;

Table 60. Characters and character states within the subgenus Schadonophasma.

Character	Plesiomorphic	Apomorphic
Adults		
1. Penis valve	Apical claw short	Apical claw elongate
Fourth Instar Larvae		
2. Head capsule length	Smaller	Larger
3. AS/AL	Low value	Higher value
4. Prelabral appendage	Elongate	Broad
5. Number of mandibular bristles	Lower	Higher
6. Number of anal fan setae	Lower	Higher
Egg		
7. General structure	Thin exochorion; no pattern on surface of exochorion	Thick exochorion; polygonal pattern on surface of exochorion

genera to which Chaoborus is more closely related to than Eucorethra. It is almost certain therefore that the large size of Schadonophasma members as a group and those of C. cooki and C. nyblaei in particular represents an apomorphic condition. In this presentation I have used larval head capsule length to represent the overall larger size of the species.

I have already discussed above the interpretation of AS/AL and prelabral appendage shape.

The high number of mandibular fan bristles of some members of C. trivittatus probably represents the apomorphic end of a morphocline. Mochlonyx fourth instar larvae have six to seven bristles in the mandibular fan (Cook, 1956; O'Connor, 1959), and no other Chaoborus species have members exhibiting such large numbers of mandibular fan bristles.

Some fourth instar larvae of C. trivittatus and C. cooki and all those of C. nyblaei have a larger number of anal fan setae than other Chaoborus species. Mochlonyx fourth instar larvae have 28-30 anal fan setae and Eucorethra underwoodi 32 (Cook, 1956). These ex-group comparisons would suggest that only the high number of anal fan setae of C. cooki and C. nyblaei are apomorphic. However, some evidence would suggest that the evolution of changes in number of anal fan setae is more complex. From observations of the swimming behavior of Chaoborus larvae it is clear that the anal fan functions as a fulcrum against which the larvae can push in a forward motion. It would seem reasonable therefore to suggest that if there are developmental restrictions on the size of individual anal fan setae, the number of anal fan setae may be related to the size of the species

and that these two characters coevolved. Distribution of number of anal fan setae relative to range of head capsule length for species of Chaoborus for which these data are available (Fig. 37) would support this hypothesis. These two characters would generally, therefore, not give independent evidence of phyletic relationships. However, it is also apparent from Figure 37 that the relationship is not a constant one. Although this may be due to inadequate sampling for some species, it is probable that other factors are also important in the evolution of number of anal fan setae. For example, even though there is no signficant difference in head capsule length of C. cooki and C. nyblaei fourth instar larvae, number of anal fan setae does significantly differ. I have therefore interpreted the large number of anal fan setae as autapomorphic for C. nyblaei.

The egg structure and type of egg mass of C. trivittatus is extremely similar to those of species of Chaoborus s. str.. Because Chaoborus s. str. is the sister group of Schadonophasma it is probable that the condition found in C. trivittatus represents the plesiomorphic state within Schadonophasma. However it is possible that the character state of C. trivittatus represents a convergence with species of Chaoborus s. str.. A 'layer of jelly-like substance' or 'thin gelatinous sheath' around individual eggs (= thick exochorion?) of some species has been described (Sikorowa, 1973; MacDonald, 1956; McGowan, 1976) and if these features are homologous with those of C. cooki and C. nyblaei these might be considered plesiomorphic within Schadonophasma. However, the eggs of these other species of Chaoborus need to be better studied before such inferences can be made.

The proposed phylogeny of the species of Schadonophasma is given in Figure 38.

7.5 Zoogeography and Speciation Events

Hennig (1966b) has shown that zoogeographic inferences are dependent upon accurate interpretation of the evolutionary relationships of organisms. Because it seems likely that detailed study of *Chaoborus* species, both extant and fossil, will alter the phylogeny of *Chaoborus* as proposed here, I will not discuss the zoogeography of the genus. However, the inferred sister group relationship between *Schadonophasma* and *Chaoborus s. str.* is probably correct.

Because all extant species of *Schadonophasma* and *Chaoborus s. str.* are found only in northern temperate regions it would be reasonable to assume that the ancestor which gave rise to extant species of *Schadonophasma* was present in the northern temperate region. Distributions of species of *Chaoborus s. str.* give no clues where specifically this ancestor may have arisen.

In the following discussion of the speciation event giving rise to *C. cooki* and *C. nyblaei*, I have assumed that *C. nyblaei* has had or does have a continuous Palaearctic distribution. However, future work may indicate that *C. nyblaei* has been and is presently restricted to Fennoscandia. A more likely explanation of the speciation event giving rise to *C. cooki* and *C. nyblaei* would then suggest disperal of adults (or possibly desiccation resistent eggs on the feet of migrating shorebirds) took place over the North Atlantic during a past period of climatic amelioration.

There are two equally probable zoogeographic interpretations of the history of Schadonophasma species.

The first suggests that the ancestor of extant Schadonophasma species was Holarctic in distribution. A split of its populations into Nearctic and Palaearctic elements resulted in the lineage giving rise to C. trivittatus and to the ancestor of C. cooki and C. nyblaei (hereafter referred to as C. cooki-nyblaei). The Palaearctic species then reinvaded North America and subsequently was split into Palaearctic and Nearctic populations which gave rise to C. nyblaei and C. cooki respectively. The model only requires allopatric speciation and dispersal to have taken place. A land bridge between Asia and North America is known to have appeared and disappeared a number of times during the Tertiary and Quaternary (Hopkins, 1967, 1972) which could have provided, during certain periods, a barrier to reproduction between Asian and North American populations.

The second zoogeographic hypothesis suggests that the ancestor of extant Schadonophasma species arose in North America and speciated in this area to give rise to the lineages resulting in C. trivittatus and C. cooki-nyblaei. Although an allopatric speciation model might explain the speciation event in North America resulting in the lineages which gave rise to C. trivittatus and C. cooki-nyblaei, it seems most likely that the invasion into temporary waters by C. cooki-nyblaei was not the result of geographical isolation. Although the lineage might have invaded temporary ponds because of competition with other Chaoborus species as a geographic isolate, it seems more likely that, especially considering the degree to which C. trivittatus and other Chaoborus species can coexist (Stahl, 1966), this would not result in

a speciation event. It is also difficult to imagine two isolated geographical areas which contained populations of the ancestral species, one of which contained only temporary waters conducive to the evolution of a temporary pond species.

The available data for Schadonophasma species allow for a hypothesis of sympatric speciation. The following are hypothesized events as indicated by this study of Schadonophasma species and features of species of Chaoborus s. str..

The Nearctic species ancestral to extant Schadonophasma species inhabited permanent waters with fourth instar larvae as the overwintering stage. Upon emergence of adults in spring, the males formed swarms on the periphery of the permanent water body and mated with females after these emerged. These are features of C. trivittatus and those species of Chaoborus s. str. for which this information is available and are therefore plesiomorphic characteristics of Schadonophasma. As previously shown for the two species C. trivittatus and C. americanus which overwinter as fourth instar larvae in permanent ponds (pg. 158), the dispersing females occasionally laid eggs in temporary ponds. Eggs which hatched resulted in larvae which could not survive overwintering in this habitat. This type of egg was strongly selected against, as all larvae which hatched would die in temporary ponds. Tauber et al. (1977) have shown that mutation of a single allele can result in the appearance of diapause in individuals of a population. If this feature is controlled by a single gene in Schadonophasma species, crosses of male C. trivittatus and female C. cooki resulting in diapausing eggs, would suggest that the allele

for diapausing eggs is dominant. I have assumed this to be the situation in the following discussion. The primitive non-diapausing egg is represented by autosomal recessive alleles aa. Mutation resulted in the production of a dominant Aa, producing diapausing eggs. A female carrying these genes laid her eggs in a temporary pond, which then diapaused in this habitat. Resistance to complete desiccation might not have evolved at this stage because, at least for the temporary ponds I investigated, the bottoms were quite moist; probably in some ponds, moist enough to prevent desiccation of eggs. Larvae which hatched out in spring from these overwintered eggs would mature to adulthood at a later time than would those in permanent ponds which emerge as adults early in spring. This might give at least a certain degree of temporal isolation. However, as discussed above (pg. 152), C. trivittatus might be multivoltine in certain regions and this might have provided some temporal overlap between two populations of the ancestral species.

The adults which emerged from the temporary pond would, as did the parent population in permanent ponds or lakes, have swarmed and mated at the pond periphery. This homogamic behavior led to further segregation of populations and ensured an increase in numbers of individual carrying this gene. The resultant adults would carry the alleles: AA or Aa. Any aa eggs laid in temporary ponds would be eliminated as larvae. AA or Aa eggs subsequently laid in permanent ponds would survive and hatch in the spring as first instars but any other Chaoborus larvae, if present, would be fourth instar and these first instars would probably be cannibalized. To hypothesize the removal of heterozygotes from the temporary pond lineage (and therefore

the continued production of aa), I suggest that the allele A became associated with co-dominant or recessive features conducive to temporary pond existence and therefore, as the temporary pond populations adapted to the temporary pond environment, heterozygotes were selected against. Adult behavior and comparatively reduced ovarian development of extant C. cooki may be examples of such adaptations but these also may have evolved after the speciation had occurred.

Through temporal disjunction of mating periods, homogamic mating, complete selection against overwintering larvae in temporary ponds and partial selection against heterozygotes in temporary ponds and overwintering eggs in permanent ponds, the two lineages giving rise to C. trivittatus and C. cooki-nyblaei became genetically isolated. These suggested events are summarized in Figure 39.

C. cooki-nyblaei invaded the Palaearctic region and subsequent barriers to reproduction, as described for the first zoogeographic hypothesis, resulted in isolated populations which gave rise to C. cooki and C. nyblaei.

The sympatric speciation model is dependent at least on the assumption that C. nyblaei does in fact overwinter as an egg. Although this was inferred from available data I have no direct evidence that this is so. Study of the life cycle of C. nyblaei would therefore provide a test of this hypothesis. If study of the populations I have described as 'Populations incertae sedis' show these to be one or more new species, this may provide additional criteria for testing this proposal of sympatric speciation.

8. Concluding Remarks

On the basis of their work, taxonomists should indicate particularly fruitful areas for future research: those concerned primarily with the group studied in particular, and those concerned with systematic problems in general.

Because of the paucity of museum material of specimens of Schadonophasma, future endeavors relating to the systematics of the subgenus must await further collections. Some details concerning the bionomics of species may bear further investigation, as indicated in the text. In particular, investigation of the life cycle of C. nyblaei and the specific affinities of the 'populations incertae sedis' may provide additional insights into the systematics of species of Schadonophasma. The phyletic relationships of species of Chaoborus are yet poorly known. Fossil species and extant species from the southern hemisphere are particularly in need of study and the entire genus is worthy of a complete revision.

In general, this study suggests that investigation of the bionomics of species of some groups may provide additional tests of the sympatric speciation model. Because of domination of evolutionary concepts by the allopatric speciation model, the full implications and requirements of the sympatric speciation model are poorly understood. These aspects of the model can only become clear when additional information on bionomics of organisms which may have speciated sympatrically become available.

As is well illustrated by the work by Bush (1975b) on tephritid fruit flies, a sympatric speciation model can only be justifiably invoked from a solid base of bionomic data. Although allopatric

speciation has in the past been the favored hypothesis to explain differentiation of organisms, it is also evident that only morphological and distributional data are available for most organisms. Therefore, until adequate bionomic data are available for a large array of taxonomic groups it will be difficult to estimate the frequency of occurrence of sympatric speciation. As discussed by Bush (1975a), sympatric speciation occurs under special genetic and environmental conditions. It seems clear that in certain groups (mammals, birds, and carabid beetles) such conditions are rarely, if ever, met. In the genus Chaoborus, considering the similarity of the life cycle of most species, it appears that sympatric speciation occurs in lesser frequency than does allopatric speciation. Nevertheless, some groups, like some species groups of tephritid flies, appear to be more prone to speciate sympatrically. This pattern suggests, therefore, that systematists should not apply the most common mode of speciation to all taxonomic groups under investigation. Rather, each speciation model should be based on the data available for that group.

An aspect not explicitly clear in previous discussions of sympatric speciation concerns the phyletic relationships and zoogeography of the organisms concerned - essential considerations in any speciation model. This study of Schadonophasma provides an example of how zoogeographic considerations may provide additional criteria for elucidation of sympatric speciation.

In conclusion, it is the intensive study of only a few closely related species, as here reported for the subgenus Schadonophasma, which can most fruitfully provide the basic information necessary to test hypotheses of sympatric speciation.

References

References

Aitken, T.H.G. 1954. The Culicidae of Sardinia and Corsica (Diptera). Bulletin of Entomological Research 45:437-494.

Akehurst, S.C. 1922. Larva of Chaoborus crystallinus (De Geer) (Corethra plumicornis F.). Journal of the Royal Microscopical Society 15:341-372.

Allan, J.D. 1973. Competition and the relative abundances of two cladocerans. Ecology 54:484-498.

Anderson, R.S. and L.G. Raasveldt. 1974. Gammarus predation and the possible effects of Gammarus and Chaoborus feeding on the zooplankton composition in some small lakes and ponds in western Canada. Canadian Wildlife Service, Occasional Paper Number 18, 23 pp.

Ashlock, P.D. 1974. The uses of cladistics. Annual Review of Ecology and Systematics 5:81-99.

Atchley, W.R., C.T. Gaskins, and D. Anderson. 1976. Statistical properties of ratios. I. Empirical results. Systematic Zoology 25:137-148.

Balvay, G. 1977a. Détermination des larves de Chaoborus (Diptera, Chaoboridae) rencontrées en France. Annales d'hydrobiologie 8:27-32.

Balvay, G. 1977b. Morphologie des stades larvaires de Chaoborus flavicans (Diptera chaoboridae) en France. Annales d'hydrobiologie 8:163-177.

Balvay, G. 1977c. Nouvelle interprétation de la signification de certains appendices céphaliques et de la morphologie de la mandibule chez la larve de premier stade de Chaoborus flavicans Meigen (Diptera, Chaoboridae). Annales d'hydrobiologie 8:179-189.

Balvay, G. 1977d. Le cycle biologique de Chaoborus flavicans (Diptera, Chaoboridae) dans le lac du Morillon (Haute-Savoie, France). Annales d'hydrobiologie 8:191-218.

Beck, A.P., G.V. Poje and W.T. Waller. 1975. A laboratory study on the effects of the exposure of some entrainable Hudson River biota to hydrostatic pressure regimes calculated for the proposed Cornwall pumped-storage plant. In Fisheries and Energy production: a symposium. Lexington Books. Lexington, Massachusetts, 300 pp.

Belkin, J.N. and S.J. Heinemann, 1975. Collection records of the project "Mosquitoes of Middle America" 3. Bahama Is. (BAH), Cayman Is. (CAY), Cuba (CUB), Haiti (HAC, HAR, HAT) and Lesser Antilles (LAR). Mosquito Systematics 7:367-393.

Belkin, J.N. and S.J. Heinemann, 1976. Collection records of the project "Mosquitoes of Middle America" 6. Southern Lesser Antilles: Barbados (BAR), Dominica (DOM), Grenada (GR, GRR), St. Lucia (LU), St. Vincent (VT). Mosquito Systematics 8:237-297.

Belkin, J.N., S.J. Heinemann, and W.A. Page. 1970. The Culicidae of Jamaica (Mosquito Studies. XXI). Contributions of the American Entomological Institute 6:1-458.

Berg, K. 1937. Contributions to the biology of Corethra Meigen (Chaoborus Lichtenstein). Kongelige Danske Videnskabernes Selskabs. Biologiske Meddelelser 13(11):1-101.

Blanchard, R. 1905. Les moustiques histoire naturelle et medicale. F.R. de Rudeval, Paris, xiii+673 pp.

Bonomi, G. 1962. La dinamica produttiva delle principali popolazioni macrobentoniche del Lago di Varese. Memorie dell'Istituto Italiano di Idrobiologia 15:207-254.

Bradshaw, W.E. 1973. Homeostasis and polymorphism in vernal development of Chaoborus americanus. Ecology 54:1247-1259.

Brown, W.J. 1959. Taxonomic problems with closely related species. Annual Review of Entomology 4:77-98.

Brundin, L. 1972. Evolution, causal biology, and classification. Zoologica Scripta 1:107-120.

Brunetti, E. 1911. Further notes on synonymy in Corethrinae. Records of the Indian Museum, Calcutta 6:227-229.

Brydon, H.W. 1956. The Clear Lake Gnat and its control in Clear Lake, California during 1954. Journal of Economic Entomology 43:206-209.

Bush, G.L. 1975a. Modes of animal speciation. Annual Review of Ecology and Systematics 6:339-364.

Bush, G.L. 1975b. Sympatric speciation in phytophagous parasitic insects. In Evolutionary strategies of parasitic insects and mites. Plenum Press, New York, xi+224 pp.

Chaston, I. 1969. The light threshold controlling the vertical migration of Chaoborus punctipennis in a Georgia impoundment. Ecology 50:916-920.

Cleugh, T.R. and B.W. Hauser. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. Journal of the Fisheries Research Board of Canada 28:129-137.

Cook, E.F. 1956. The Nearctic Chaoborinae (Diptera: Culicidae). University of Minnesota Agricultural Experiment Station Technical Bulletin 218, 102 pp.

Corbet, P.S. 1958. Lunar periodicity of aquatic insects in Lake Victoria. Nature 182:330-331.

Darlington, P.J. Jr. 1970. A practical criticism of Hennig-Brundin "Phylogenetic Systematics" and Antarctic biogeography. Systematic Zoology 19:1-18.

Deckart, M. 1958. Die Larve der Büschelmücke. Mikrokosmos 47:265-271.

Deevy, E.S. 1942. Studies on Connecticut lake sediments. III. The biostratonomy of Linsley Pond. American Journal of Science 240:233-264, 313-324.

Deonier, C.C. 1943. Biology of the immature stages of the Clear Lake gnat (Diptera, Culicidae). Annals of the Entomological Society of America 36:383-388.

Dickenson, W.E. 1944. The mosquitoes of Wisconsin. Bulletin of the Public Museum of the City of Milwaukee 8:269-365.

Dodson, S.I. 1970. Complementary feeding niches sustained by size-selective predation. Limnology and Oceanography 15:131-137.

Downes, J.A. 1974. The feeding habits of adult Chironomidae. Entomologisk Tidskrift 95, Supplement:84-90.

Dyar, H.G. 1902. Illustrations of the larvae of North American Culicidae. Journal of the New York Entomological Society 10:194-201, pls. 16-19.

Dyar, H.G. 1905. Our present knowledge of North American corethrid larvae. Proceedings of the Entomological Society of Washington 7:13-16.

Dyar, H.G. and R.C. Shannon. 1924. The American Chaoborinae (Diptera, Culicidae). Insecutor Inscitiae Menstruus 12:201-216.

Edwards, F.W. 1920. The British Chaoborinae and Dixinae (Diptera, Culicidae). Entomologist's Monthly Magazine 56:264-270.

Edwards, F.W. 1923. Oligocene mosquitoes in the Brisith Museum; with a summary of our present knowledge concerning fossil Culicidae. Quarterly Journal of the Geological Society of London 79:139-155.

Edwards, F.W. 1930. Notes on exotic Chaoborinae, with descriptions of new species (Diptera, Culicidae). Annals and Magazine of Natural History 6:528-540.

Edwards, F.W. 1932. Diptera. Family Culicidae. Genera Insectorum 194:1-258.

Eggleton, F.E. 1932. Limnetic distribution and migration of Corethra larvae in two Michigan lakes. Papers of the Michigan Academy of Science, Arts and Letters 15:361-388.

Fedorenko, A.Y. 1975a. Instar and species-specific diets in two species of Chaoborus. Limnology and Oceanography 20:238-249.

Fedorenko, A.Y. 1975b. Feeding characteristics and predation impact of Chaoborus (Diptera, Chaoboridae) larvae in a small lake. Limnology and Oceanography 20:250-258.

Fedorenko, A.Y. 1975c. Development patterns and their possible adaptive significance in three types of fourth instar Chaoborus larvae. Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:3098-3105.

Fedorenko, A.Y. and M.C. Swift. 1972. Comparative biology of Chaoborus americanus and Chaoborus trivittatus in Eunice Lake, British Columbia. Limnology and Oceanography 17:721-730.

Felt, E.P. 1904. Mosquitos or Culicidae of New York State. New York State Museum, Bulletin 79, Entomology 22:241-400, 57 ps.

Felt, E.P. 1905. Studies in Culicidae. New York State Museum, Bulletin 97, Entomology 24:442-497, 462-564, pls. 1-19.

Frankenberg, G. von. 1915. Die Schwimmblasen von Corethra. Zoologische Jahrbücher für Allegemeine Zoologie und Physiologie der Tiere 35:505-592.

Frankenberg, G. von. 1937. Die "Weisse Mückenlarve" (Corethra). Mikrokosmos 30:57-63.

Freitag, R. 1965. A revision of the North American species of the Cicindela maritima group with a study of hybridization between Cicindela duodecimguttata and oregona. Quaestiones Entomologicae 1:87-170.

Frey, D.G. 1955. Längsee: A history of meromixus. Memorie dell' Istituto Italiano di Idrobiologia. Supplement 8:141-164.

Frey, D.G. 1962. Cladocera from the Eemian Interglacial of Denmark. Journal of Paleontology 36:1133-1154.

Giles, G.M. 1902. A handbook of the gnats or mosquitoes. Second edition, John Bale, Sons and Danielsson, Ltd., London. xi+530 pp., 17 pls.

Giles, G.M. 1904. Cold weather mosquito notes from the united provinces - North-west India. Journal of Tropical Medicine 7:49-52.

Gimmerthal, B.A. 1845. Erster Beitrag zu einer Kunftig zu Bearbeitenden Dipterologie Russlands. Bulletin de la Société Impériale des Naturalistes de Moscou 18:287-331.

Goff, A.M. 1972. Feeding of adult Chironomus riparius Meigen. Mosquito News 32:243-244.

Goldspink, C.R. and D.B.C. Scott. 1971. Vertical migration of Chaoborus flavicans in a Scottish Loch. Freshwater Biology 1:411-421.

Goulden, C.E. 1966a. La Aguada de Santa Ana Vieja: an interpretative study of the cladoceran microfossils. Archiv für Hydrobiologie 62:373-404.

Goulden, C.E. 1966b. The animal microfossils of Laguna de Petenxil, Guatemala. Conneticut Academy of Arts and Sciences, Memoir 17:84-120.

Green, J. 1972. Ecological studies on crater lakes in West Cameroon zooplankton of Barombi Mbo, Mboandong, Lake Kotto and Lake Soden. Journal of Zoology. Proceedings of the Zoological Society of London 166:283-301.

Green, J. and J.O. Young. 1976. The larva of the lake fly Chaoborus pallidipes Theobald (Diptera: Chaoboridae) from Kenya. Journal of Natural History 10:463-467.

Green, J., S.A. Corbet, and E. Betney, 1973. Ecological studies on crater Lakes in West Cameroon. The blood of endemic cichlids in Barombi Mbo in relation to stratification and their feeding habits. Journal of Zoology. Proceedings of the Zoological Society of London 170:299-308.

Griffiths, G.C.D. 1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. Junk, The Hague. 340 pp.

Griffiths, G.C.D. 1974. On the foundations of biological systematics. Acta Biotheoretica 13:85-131.

Hamilton, A.L. 1971. Zoobenthos of fifteen lakes in the Experimental Lakes Area, northwestern Ontario. Journal of the Fisheries Research Board of Canada 28:257-263.

Hearle, E. 1928. List of mosquitoes of British Columbia. Recorded to December 31, 1926. Entomological Society of British Columbia, Proceedings 24:11-19.

Hecht, M.K. and J.L. Edwards. 1977. The methodology of phylogenetic inference above the species level. In Hecht, M.K., P.C. Goody, and B.M. Hecht (editors). Major patterns in vertebrate evolution. Volume 14. NATO Advanced Study Institute Series A. Plenum Press, New York and London.

Heinemann, S.J. and J.N. Belkin. 1977a. Collection records of the project "Mosquitoes of Middle America" 7. Costa Rica (CR). Mosquito Systematics 9:237-287.

Heinemann, S.J. and J.N. Belkin. 1977b. Collection records of the project "Mosquitoes of Middle America" 8. Central America: Belize (BH), Guatemala (GUA), El Salvador (SAL), Honduras (HON), Nicaragua (NI, NIC). Mosquito Systematics 9:403-454.

Hennig, W. 1966a. Phylogenetic systematics. University of Illinois Press, Urbana. 263 pp.

Hennig, W. 1966b. The Diptera fauna of New Zealand as a problem in systematics and zoogeography. Pacific Insects, Monograph 9, 81 pp.

Herms, W.B. 1937. The Clear Lake gnat. University of California College of Agriculture Agricultural Experiment Station Berkeley, California, Bulletin 607:1-22.

Heyden, C. von. 1862. Gliederthiere aus der Braunkohle des Niederrhein's, der Wetterau und der Röhn. Palaeontographica 10:62-82, pl. 10.

Hinton, H.E. 1969b. Some structures of insects as seen with the scanning electron microscope. Micron 1:84-108.

Hinton, H.E. and M.W. Service. 1969a. The surface structure of aedine eggs as seen with the scanning electron microscope. Annals of Tropical Medicine and Parasitology 63:409-411.

Hirvenoja, M. 1960. Ökologische Studien über die Wasserinsekten in Riihimäki (Südfinnland). I. Chaoborinae (Dipt., Culicidae). Suomen Hyönteistieteellinen Aikakauskirja (= Annales Entomologici Fennici) 26:31-44.

Hirvenoja, M. 1961. Weitere Studien über Chaoborinen (Dipt., Culicidae). Beschreibung der Larve und der Puppe von Chaoborus (Schadonophasma) nyblaei Zett. IBID 27:77-83.

Hirvenoja, M. 1965. On the diel periodicity of pupal emergence of Chaoborus crystallinus DeG. (Dipt., Culicidae). IBID 31:73-75.

Hitchcock, S.W. 1965. The seasonal fluctuation of limnetic Chaoborus punctipennis and its role as a pest in drinking water. Journal of Economic Entomology 58:902-904.

Hofmann, W. 1971. Die postglaziale Entwicklung der Chironomiden und Chaoborus - fauna (Dipt.) des Schöhsees. Archiv für Hydrobiologie, Supplement 40:1-74.

Hongve, D. 1975. On the ecology and distribution of Chaoborus (Chaoboridae, Diptera) from the Upper Romerike District, south-east Norway. Norwegian Journal of Entomology 22:49-57.

Hopkins, D.M. 1967. The Cenozoic history of Beringia - a synthesis, pp. 451-484. In The Bering Land Bridge, Stanford University Press, Stanford. 495 pp.

Hopkins, D.M. 1972. The paleogeography and climatic history of Beringia during Late Cenozoic time. Inter-nord 12:121-150.

Hope, F.W. 1847. Observations on the fossil insects of Aix in Provence, with descriptions and figures of three species. Transactions of the Entomological Society of London 4:250-255.

Horsfall, W.R. and M.C. Ronquillo. 1970. Genesis of the reproductive system of mosquitoes. II. Male Aedes stimulans (Walker). Journal of Morphology 131:329-358.

Hubbs, C. and A.E. Peden. 1969. Gambusia georgei sp. nov. from San Marcos, Texas. Copeia 1962(2):357-364.

Hull, D.L. 1970. Contemporary systematic philosophies. Annual Review of Ecology and Systematics 1:19-54.

James, H.G. 1957. Mochlonyx velutinus (Ruthe) (Diptera: Culicidae), an occasional predator of mosquito larvae. Canadian Entomologist 89:470-480.

James, H.G. and B.C. Smith. 1958. Observations on three species of Chaoborus Licht. (Diptera: Culicidae) at Churchill, Manitoba. Mosquito News 18:242-248.

James, H.G., G. Wishart, R.E. Bellamy, M. Maw and P. Belton. 1969. An annotated list of mosquitoes of southeastern Ontario. Proceedings of the Entomological Society of Ontario 100:200-230.

Jenkins, D.W. and K.L. Knight. 1950. Ecological survey of the mosquitoes of Great Whale River, Quebec. Proceedings of the Entomological Society of Washington 52:209-223.

Johannsen, O.A. 1903. Aquatic nematocerous Diptera. New York State Museum, Bulletin 68, Entomology 18:328-486.

Johannsen, O.A. 1934. Aquatic Diptera. Part I. Cornell University Agricultural Experiment Station, Memoir 164:1-71, pls. 1-24.

Johnson, D.L. 1977. The Late Quaternary climate of coastal California: evidence for an Ice Age refugium. Quaternary Research 8:154-179.

Juday, C. 1921. Quantitative studies of the bottom fauna in the deeper waters of Lake Mendota. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 20:461-493.

Kavanaugh, D.H. 1972. Hennig's principles and methods of phylogenetic systematics. The Biologist 54:115-127.

Kim, K.C., B.W. Brown and E.F. Cook. 1966. A quantitative taxonomic study of the Hoplopleura hesperomydis complex (Anoplura, Hoplopleuridae), with notes on a posteriori taxonomic characters. Systematic Zoology 15:24-45.

Knight, K.L. 1971a. A mosquito taxonomic glossary. VII. The pupa. Mosquito Systematic Newsletter 3:42-65.

Knight, K.L. 1971b. Comparative anatomy of the mandible of the fourth instar mosquito larva (Diptera: Culicidae). Journal of Medical Entomology 8:189-205.

Knight, K.L. and J.L. Laffoon. 1971. A mosquito taxonomic glossary. VIII. The larval chaetotaxy. Mosquito Systematic Newsletter 3:160-194.

Kruger, E.J. 1973. Autumn feeding cycle of the bull-dog Fish Gnathonemus macrolepidotus (Pisces, Mormyridae). Zoologica Africana 8:25-34.

Laffoon, J.L. and K.L. Knight. 1971. A mosquito taxonomic glossary. VI. Female genitalia. Mosquito Systematic Newsletter 3:32-41.

Lane, J. 1951. Synonymy of Neotropical Culicidae. Proceedings of the Entomological Society of Washington 53:333-336.

Lane, J. 1953. Neotropical Culicidae. Volume 1. University of Sâo Paulo, Sâo Paula, 548 pp.

LaRow, E.J. 1968a. A persistent diurnal rhythm in Chaoborus larvae. I. The nature of the rhythmicity. Limnology and Oceanography 13:250-256.

LaRow, E.J. 1969. A persistent diurnal rhythm in Chaoborus larvae. II. Ecological significance. Limnology and Oceanography 14:213-218.

LaRow, E.J. and G.R. Marzolf. 1970. Behavioral differences between 3rd and 4th instars of Chaoborus punctipennis Say. The American Midland Naturalist 84:428-436.

Lewis, W.M. Jr. 1975. Distribution and feeding habits of a tropical Chaoborus population. Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:3106-3119.

Lindquist, A.W. and C.C. Deonier, 1942a. Emergence habits of the Clear Lake gnat. Journal of the Kansas Entomological Society 15:109-120.

Lindquist, A.W. and C.C. Deonier. 1942b. Flight and oviposition habits of the Clear Lake gnat. Journal of Economic Entomology 35:411-415.

Lindquist, A.W. C.C. Deonier and J.E. Hancey. 1943. The relationship of fish to the Clear Lake gnat, in Clear Lake, California. California Fish and Game 29:196-202.

Lindquist, A.W., A.R. Roth and J.R. Walker. 1951. Control of the Clear Lake gnat in California. Journal of Economic Entomology 44:572-577.

Loew, H. 1862. Diptera Americae septentrionalis indigena. Berliner Entomologische Zeitschrift 6:185-232.

MacDonald, W.W. 1953. Lake-flies. Uganda Journal 17:124-134.

MacDonald, W.W. 1956. Observations on the biology of chaoborids and chironomids in Lake Victoria and on the feeding habits of the "elephant-snout fish" (Mormyrus kannume Forsk.). Journal of Animal Ecology 25:36-53.

Mägdefrau, K. 1968. Paläobiologie der Pflanzen. Gustav Fischer Verlag, Stuttgart. 549 pp.

Main, R.A. 1953. A limnological study of Chaoborus (Diptera) in Hall Lake, Washington. Master of Science dissertation, University of Washington, Seattle, 106 pp.

Malueg, K.W. 1966. An ecological study of Chaoborus. Doctor of Philosophy dissertation, University of Wisconsin, Madison, 255 pp.

Malueg, K.W. and A.D. Hasler. 1967. Echo sounder studies on diel vertical movements of Chaoborus larvae in Wisconsin (U.S.A.) lakes. Internationale Vereinigung fur Theoretische und Angewandte Limnologie 16:1697-1708.

Marland, F.C. 1967. The history of Mountain Lake, Giles County, Virginia: an interpretation based on paleolimnology. Doctor of Philosophy dissertation, Virginia Polytechnic Institute, Blacksburg, 138 pp.

Martini, E. 1931. Culicidae. Die Fliegen der Palaearktischen Region 3(11,12):1-398, 1 pl.

Maslin, T.P. 1952. Morphological criteria of phyletic relationships. Systematic Zoology 1:49-70.

Matheson, R. 1944. Handbook of the mosquitos of North America. Comstock, Ithaca. 314 pp., 33 pls.

Matheson, R. 1945. Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. Second fascicle. Family Culicidae, the mosquitoes. State of Connecticut State Geological and Natural History Survey Bulletin Number 68. 48 pp.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, New York. 428 pp. xi+428 pp.

Mayr, E. 1974. Cladistic analysis or cladistic classification? Zeitschrift für Zoologische Systematik und Evolutionsforschung 12:94-128.

McCloy, J.S. 1950. A preliminary study of the Chaoborinae of Utah. Master of Science dissertation, University of Utah, Salt Lake City, 43 pp., 4 pls.

McGowan, L.M. 1972. Description of the larvae of Chaoborus (Neochaoborus) anomalus Edwards and Chaoborus (Sayomyia) ceratopogones Theobald (Diptera Chaoboridae) from Lake George, Uganda, and their morphological variation in other African lakes. Revue de Zoologie et de Botanique Africaines 85:357-368.

McGowan, L.M. 1974. Ecological studies on Chaoborus (Diptera, Chaoboridae) in Lake George, Uganda. Freshwater Biology 4:483-505.

McGowan, L.M. 1975. The occurrence and behavior of adult Chaoborus and Procladius (Diptera: Nematocera) from Lake George, Uganda. Zoological Journal. Linnean Society 57:321-334.

McGowan, L.M. 1976. Description of the adults and immature stages of Chaoborus (Sayomyia) edulis Edwards (Diptera Chaoboridae) from Ghana, West Africa. Revue de Zoologie Africaine 90:291-305.

Meinert, F. 1886. De eucephale Myggelarver. Kongelige Danske Videnskabernes Selskabs Skrifter (6). Naturvidenskabelig og Matematisk aFdeling 3:369-493.

Meunier, F. 1904. Sur un Corethra de l'ambre de la Baltique (Dipt.). Bulletin de la Société Entomologique de France 1904:89-91.

Miyadi, D. 1932. Studies on the bottom fauna of Japanese lakes. VI. Lakes of southern Kyûsyû. Japanese Journal of Zoology 4:127-149.

Miyadi, D. and N. Hazama. 1932. Quantitative investigation of the bottom fauna of Lake Yogo. Japanese Journal of Zoology 4:151-211.

Miyagi, I. 1974. On a blood-sucking Corethrella sp. collected in Nagasaki, Japan (Diptera: Chaoboridae). Tropical Medicine 16:89-93.

Miyagi, I. 1975. A new species of the genus Corethrella Coquillett from Japan (Diptera: Chaoboridae). Japanese Journal of Sanitary Zoology 26:25-29.

Montchadsky, A.S. 1953. On the seasonal dimorphism of larvae of Mochlonyx culiciformis De Geer. (Diptera, Culicidae, Chaoborinae). Trudy Zoologicheskogo Instituta. Akademiy nauk SSSR 13:363-372.

Montchadsky, A.S. 1964. The role of Chaoborinae larvae (Diptera, Culicidae) in the extinction of the larvae of bloodsucking mosquitoes. Zoologicheskii Zhurnal 43:455-466.

Muttkowski, R.A. 1918. The fauna of Lake Mendota: a qualitative and quantitative survey with special reference to the insects. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 19:374-482.

Myklebust, R.J. 1966. Distribution of mosquitoes and chaoborids in Washington State, by counties. Mosquito News 26:515-519.

Nielson, E.T. and H. Greve. 1950. Studies on the swarming habits of mosquitos and other Nematocera. Bulletin of Entomological Research 41:227-258, pls. 7-8.

O'Connor, C.T. 1959. The life history of Mochlonyx cinctipes (Coquillett) (Diptera: Culicidae). Annals of the Entomological Society of America 52:519-523.

Panday, R.S. 1975. Mosquito identification studies in a savanna forest in Surinam. Mosquito News 35:141-146.

Parma, S. 1969. Notes on the larval taxonomy, ecology, and distribution of the Dutch Chaoborus species (Diptera, Chaoboridae). Beaufortia 17:21-50.

Parma, S. 1971a. The morphology of the larval instars of Chaoborus flavicans (Meigen, 1818) (Diptera, Chaoboridae). Beaufortia 18:173-182.

Parma, S. 1971b. Chaoborus flavicans (Meigen) (Diptera, Chaoboridae): an autecological study. Doctor of Philosophy dissertation, University of Groningen, Groningen, 128 pp.

Petr, T. 1972. On some factors determining the quantitative changes in chaoborids in the Volta man-made lake during the filling period. Revue de Zoologie et de Botanique Africaines 85:147-159.

Peus, F. 1934. Zur Kenntnis der Larven und Puppen der Chaoborinae (Corethrinae auct.). Archiv für Hydrobiologie 27:641-668.

Peus, F. 1967. Ptychopteridae, Chaoboridae, Dixidae, pp. 330-334. In Limnofauna Europaea. Gustav Fischer Verlag, Stuttgart. xv+474 pp.

Pope, G.E., J.C.H. Carter and G. Power. 1973. The influence of fish on the distribution of Chaoborus spp. (Diptera) and density of larvae in the Matamek River system, Québec. Transactions of the American Fisheries Society 102:707-714.

Prashad, B. 1918. Contributions to the anatomy of aquatic Diptera. 1. Larval and pupal stages of an Indian Chaoborus and Dixa. Indian Museum Records 15:153-158, p. 19.

Prest, V.K. 1969. Retreat of Wisconsin and Recent ice in North America. Map number 1257a, Geological Survey of Canada, Department of Energy, Mines and Resources, Queen's Printer, Ottawa.

Prokesova, V. 1959. Beitrag zur Artenunterscheidung und zum Vorkommen der Chaoborus - larven (Diptera). Casopis Ceskoslovenské Spolecnosti Entomologické (= Acta Societatis Entomologicae Cechosloveniae) 56:142-149.

Pucat, A.M. 1965. The functional morphology of the mouthparts of some mosquito larvae. Quaestiones Entomologicae 1:41-86.

Rapoport, E.H. 1969. Gloger's rule and pigmentation of Collembola. Evolution 23:622-626.

Reeves, B.O.K. 1973. The nature and age of the contact between the Laurentide and Cordilleran ice sheets in the Western Interior of North America. Arctic and Alpine Research 5:1-16.

Reisen, W.K. 1973. Invertebrate and chemical serial progression in temporary pool communities at Turner's Falls, Murray County, Oklahoma. Journal of the Kansas Entomological Society 46:294-301.

Rising, J.D. 1970. Morphological variation and evolution in some North American orioles. Systematic Zoology 19:315-351.

Roff, D. 1977. Dispersal in dipterans: its costs and consequences. Journal of Animal Ecology 46:443-456.

Ross, H.H. 1974. Biological systematics. Addison-Wesley Publishing Company, Inc., Reading, Massachusetts, 345 pp.

Roth, J.C. 1967. Notes on Chaoborus species from the Douglas Lake region, Michigan, with a key to their larvae (Diptera: Chaoboridae). Papers of the Michigan Academy of Science, Arts and Letters 52:63-68.

Roth, J.C. and S. Parma. 1970. A Chaoborus bibliography. Bulletin of the Entomological Society of America 16:100-110.

Saether, O.A. 1967. Variation within immature stages of Chaoborus flavicans (Meig.) (syn. Chaoborus alpinus Peus syn. nov.). Internationale Revue der Gesamten Hydrobiologie 52:573-587.

Saether, O.A. 1970. Nearctic and Palaearctic Chaoborus (Diptera: Chaoboridae). Fisheries Research Board of Canada, Bulletin 174, vii+57 pp.

Saether, O.A. 1972. VI. Chaoboridae. pp. 257-280. In Das Zooplankton de Binnengewässer. 1. Teil. Binnengewässer 26:1-294.

Saether, O.A. 1976. Two species of Chaoborus (Diptera: Chaoboridae) from Venezuela. Acta Biologica Venezuelica 9:195-212.

Sailer, R.I. and S.E. Lienk. 1954. Insect predators of mosquito larvae and pupae in Alaska. Mosquito News 14:14-16.

Schlee, D. 1966. Präparation und Ermittlung von Messwerten an Chironomidae (Diptera). Gewässer und Abswässer; eine Limnologische Schriftenreihe 41/42:169-193.

Schlee, D. 1975. Numerical phyletics: an analysis from the viewpoint of phylogenetic systematics. Entomologica Scandinavica 6:193-208.

Scudder, S.H. 1890. The Tertiary insects of North America. Report of the United States Geological Survey of the Territories 13:1-662.

Séguy, E. 1924. Les moustiques de l'Afrique mineure de l'Égypte et de la Syrie. Encyclopédie Entomologique 1:1-257.

Senior-White, R. 1927. Notes on Ceylon mosquitos, -II. The larvae of the commoner non-anopheline mosquitos. Spolia Zeylanica 14:61-76.

Serres, M. de. 1829. Géognosie des terrains du midi de France, ou tableau des principaux animaux invertébrés des terrains marins tertiaires de la France. Montpellier, Durville. 276 pp.

Shemanchuk, J.A. 1959. Mosquitoes (Diptera: Culicidae) in irrigated areas of southern Alberta and their seasonal changes in abundance and distribution. Canadian Journal of Zoology 37:899-912.

Sikorowa, A. 1964. A species new to Polish fauna - from the genus Chaoborus Licht. (Diptera). Ekologia Polska, Seria A 12:121-123.

Sikorowa, A. 1967a. Beitrag zur Systematik und Ökologie der Chaoborinae. Internationale Vereinigung fur Theoretische und Angewandte Limnologie 16:1709-1715.

Sikorowa, A. 1967b. Occurrence of Chaoborus alpinus Peus (Diptera, Culicidae), a new species in Poland. Polskie Archiwum Hydrobiologii 14:87-90.

Sikorowa, A. 1970. Discovery of a new systematical feature in larvae of the genus Chaoborus Licht. (Diptera, Culicidae). Polskie Pismo Entomologiczne 40:79-82.

Sikorowa, A. 1973. Morfologia, biologia i ekologia gatunków rodzaju Chaoborus Lichtenstein (Diptera, Chaoboridae) wystepujacych w Polsce. Zeszyty Naukowe Akademii Rolniczo-Technicznej w Olsztynie 105:1-121.

Sittler, C. 1967. Mise an évidence d'un rechauffement climatique à la limite de l'Oligocène et du Miocene. Review of Palaeobotany and Palynology 2:163-172.

Skierska, B. 1969. Larvae Chaoborinae (Diptera; Culicidae) occurring in small water reservoirs. I. Some observations on larvae of Chaoborus crystallinus (De Geer, 1776) and on the possibility of their predacity in relation to larvae of biting mosquitoes (Diptera; Culicidae, Culicinae). Institute of Marine Medicine in Gdansk, Bulletin 20:101-108.

Skierska, B. 1974. Komary (Diptera: Culicidae) zachodniej czesci wyspy Wolina i poludniowo-zachodniej czesci Uznamu. Poznańskie Towarzystwo Przyjaciół Nauk 36:1-79.

Smith, B.C. 1960a. Immature stages of Chaoborus borealis Cook (Diptera: Culicidae). Canadian Entomologist 92:396-400.

Smith, B.C. 1960b. Note on variation in larvae of Chaoborus Licht. (Diptera: Culicidae). Mosquito News 20:192.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy. The principles and practice of numerical classification. W.H. Freeman and Co., San Francisco. xv+573 pp.

Sokal, R.R. 1975. Mayr on cladism - and his critics. Systematic Zoology 24:257-262.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco. xxi+776 pp.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. Biological Reviews 37:171-214.

Stahl, J.B. 1959. The developmental history of the chironomid and Chaoborus faunas of Myers Lake. Investigations of Indiana Lakes and Streams 5:47-102.

Stahl, J.B. 1966. Coexistence in Chaoborus and its ecological significance. Investigations of Indiana Lakes and Streams 7:99-113.

Stahl, J.B. 1969. The uses of chironomids and other midges in interpreting lake histories. Mitteilungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 17:111-125.

Swift, M.C. 1975. Simulation studies of Chaoborus vertical migration. Internationale Vereinigung für Theoretische und Angewandte Limnologie 19:3120-3126.

Swift, M.C. 1976. Energetics of vertical migration in Chaoborus trivittatus larvae. Ecology 57:900-914.

Swift, M.C. and A.Y. Fedorenko. 1973. A rapid method for the analysis of the crop contents of Chaoborus larvae. Limnology and Oceanography 18:795-798.

Swift, M.C. and A.Y. Fedorenko. 1975. Some aspects of prey capture by Chaoborus larvae. Limnology and Oceanography 20:418-425.

Swüste, H.F.J., R. Cremer, and S. Parma. 1973. Selective predation by larvae of Chaoborus flavicans (Diptera, Chaoboridae). Internationale Vereinigung für Theoretische und Angewandte Limnologie 18:1559-1563.

Szalay, F.S. 1977. Ancestors, descendants, sister groups and testing of phylogenetic hypothesis. Systematic Zoology 26:12-18.

Tauber, C.A. and M.J. Tauber. 1977. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. Nature 268:702-705.

Tauber, C.A., M.J. Tauber and J.R. Nechols. 1977. Two genes control seasonal isolation in sibling species. Science 197:592-593.

Teraguchi, M. and T.G. Northcote. 1966. Vertical distribution and migration of Chaoborus flavicans larvae in Corbett Lake, British Columbia. Limnology and Oceanography 11:164-176.

Theobald, F.V. 1901a. A monograph of the Culicidae or mosquitoes. 1901-1910. Volume 1. William Clowes and Sons, Ltd., London. xviii+424 pp.

Theobald, F.V. 1901b. A monograph of the Culicidae or mosquitoes. 1901-1910. Volume 2. William Clowes and Sons, Ltd., London. viii+391 pp.

Theobald, F.V. 1903. A monograph of the Culicidae or mosquitoes. 1901-1910. Volume 3. William Clowes and Sons, Ltd., London. xvii+359 pp., 17 pls.

Theobald, F.V. 1905. Diptera. Family Culicidae. Genera Insectorum 5:1-50.

Tjønneland, A. 1958. Observations on Chaoborus edulis (Edwards) (Diptera, Culicidae). Universitetet i Bergen Arbok Naturvitenskapelig Rekke 16:1-12.

Tullock, G.S. 1934. Mosquito investigations in Alaska. Psyche 41:201-210.

Twinn, C.R., B. Hocking, W.C. McDuffie and H.F. Cross. 1948. A preliminary account of the biting flies at Churchill, Manitoba. Canadian Journal of Research 26(D):334-357.

Verbeke, J. 1957. Chaoboridae (Diptera Nematocera). Stades immatures et adultes. Exploration Hydrobiologique des Lacs Kivu, Edouard et Albert (1952-1954) 3(2):185-203.

Verbeke, J. 1958. Chaoboridae (Diptera Nematocera). Exploration du Parc National Albert, Mission G.F. De Witte (1933-1935) Fascicle 94,57 pp., 3 pls.

Vernberg, F.J. 1962. Comparative physiology: latitudinal effects on physiological properties of animal populations. Annual Review of Physiology 24:517-546.

Weismann, A. 1866. Die Metamorphose der Corethra plumicornis. Zeitschrift für Wissenschaftliche Zoologie 16:45-127.

Wesenberg-Lund, C. 1914. Bidrag til Nogle Myggeslaegters, Saerlig Mochlonyx og Corethra's Biologi. Mindeskrift. Japetus Steenstrups Fødsel. No. 34. 25 pp.

Wesenberg-Lund, C. 1919. Contributions to the knowledge of the postembryonal development of the Hydracarina. Dansk Naturhistorisk Forening 70:5-57.

Wesenberg-Lund, C. 1943. Biologie der Susswasserinsekten. Springer Verlag, Berlin. 682 pp.

Wichard, W. 1975. Zur osmoregulatorischen Anpassung von Wasserinsekten im Neusiedlersee-Gebiet. Nachrichtenblatt der Bayerischen Entomologen 24:81-87.

Wigglesworth, V.B. 1933. The function of the anal gills of the mosquito larva. Journal of Experimental Biology 10:16-26.

Wigglesworth, V.B. 1965. The principles of insect physiology. Methuen and Co., Ltd., sixth edition, London. vii+741 pp.

Williams, J.A. and J.D. Edman. 1968. Occurrence of blood meals in two species of Corethrella in Florida. Annals of the Entomological Society of America 61:1336.

Woodmansee, R.A. and B.J. Grantham. 1961. Diel vertical migrations of two zooplankters (Mesocyclops and Chaoborus) in a Mississippi lake. Ecology 42:619-628.

Zetterstedt, J.W. 1838. Dipterologis Scandinaviae. Section 3. Diptera, pp. 447-865. In Insecta Lapponica descripta, Leipzig. 1140 pp.

Zetterstedt, J.W. 1851. Diptera Scandinaviae disposita et descripta, Lund, Verfasser. 10:3711-4090.

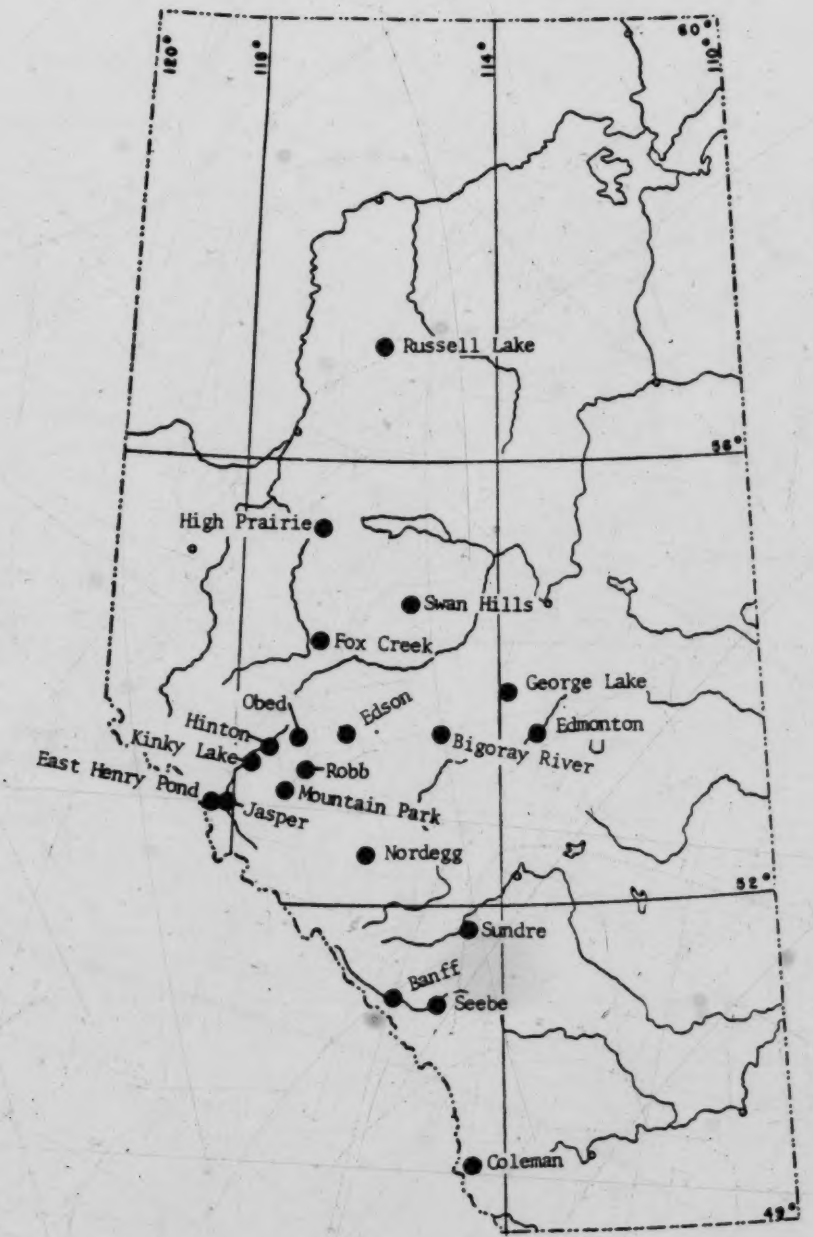


Figure 1. Place names in Alberta cited in text.

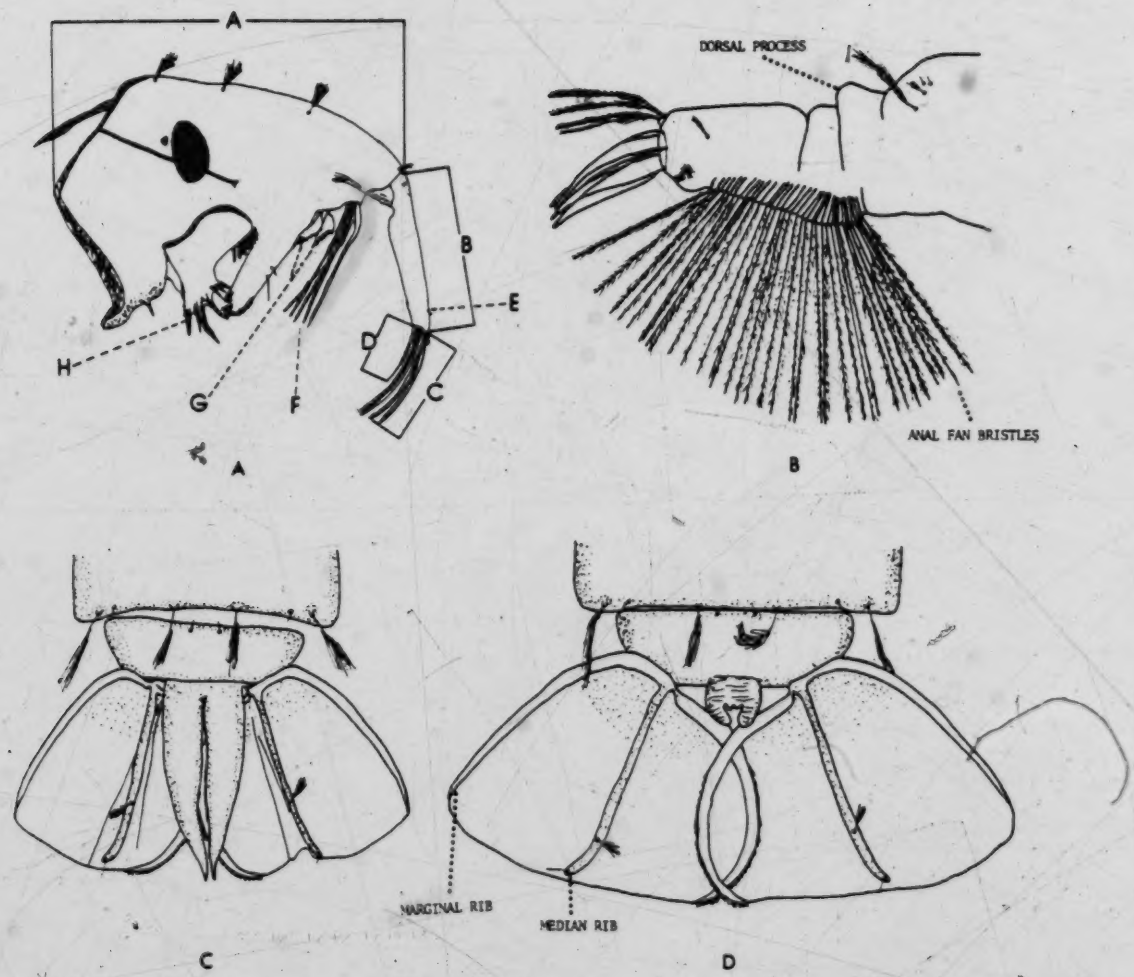
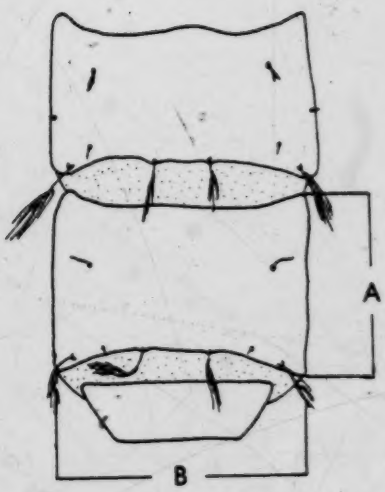
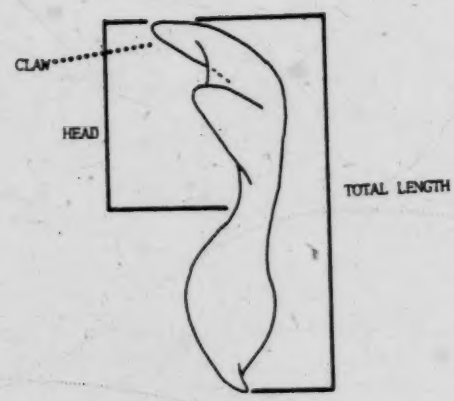


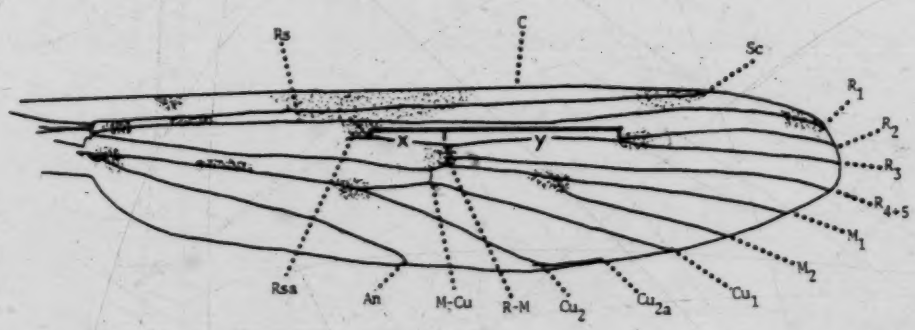
Figure 2. A. Characters and measurements of head capsule of fourth instar larva: A. Head capsule length; B. Antennal length; C. Long antennal blade length; D. Short antennal blade length; E. Antennal seta; F. Postantennal filaments; G. Prelabral appendages; H. Mandible; total length of mandibular fan bristles and labral brush setae is not shown. B. Characters of terminal abdominal segments of fourth instar larva. C. Terminalia of male pupa. D. Terminalia of female pupa. All drawings from specimens of Chaoborus cooki.



A



B



C

Figure 3. Terms and measurements of A. Terminal abdominal segments of pupa: A. Length of abdominal segment VII; B. Width of abdominal segment VII. B. Male adult penis valve. C. Wing of adult (male).

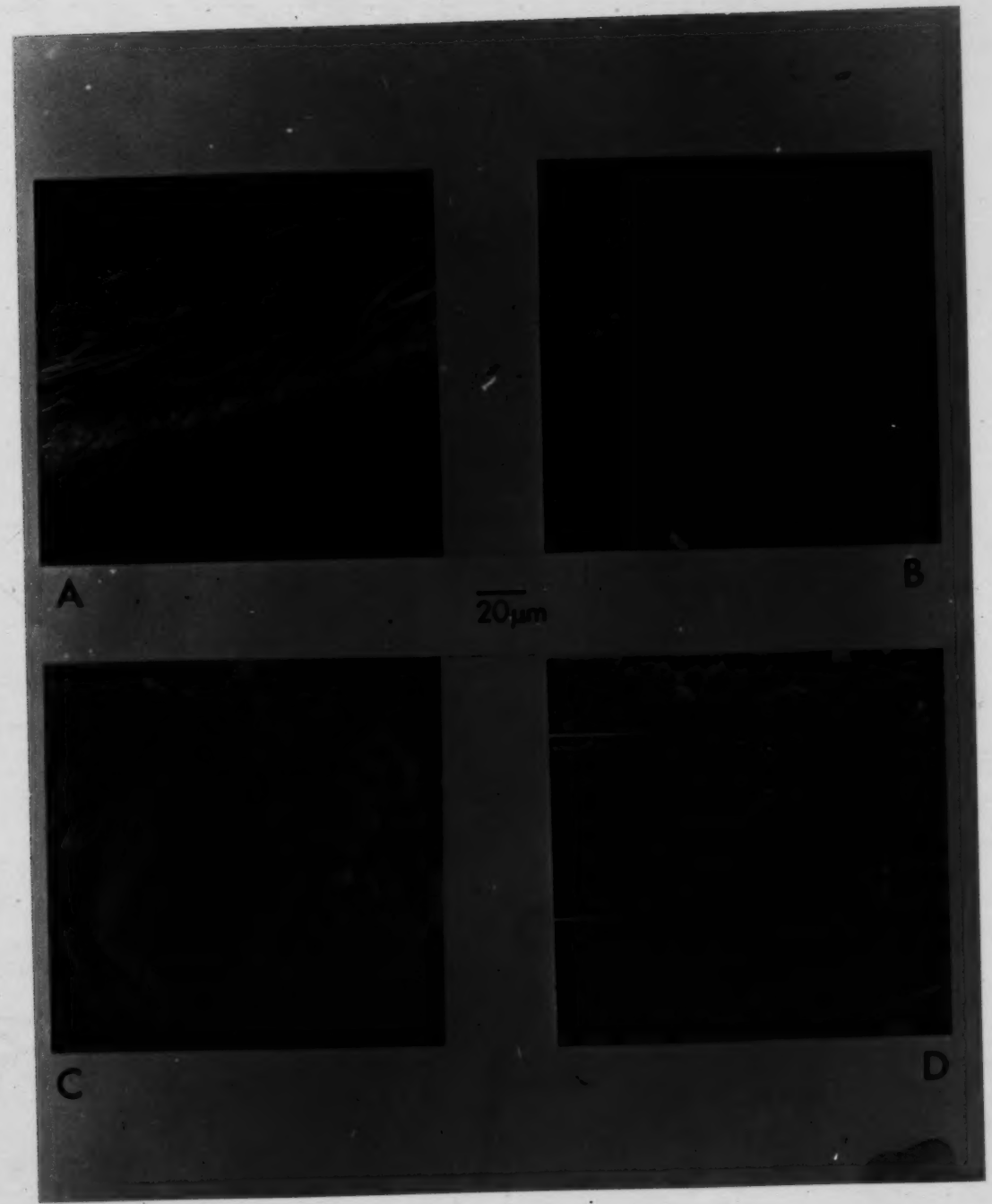


Figure 4. A. Third tarsomere of midleg of female adult. B. Microsculpture of dorsal margin of head capsule of fourth instar larva. C. Exochorion of egg of Chaoborus trivittatus. D. Exochorion of egg of Chaoborus cooki.

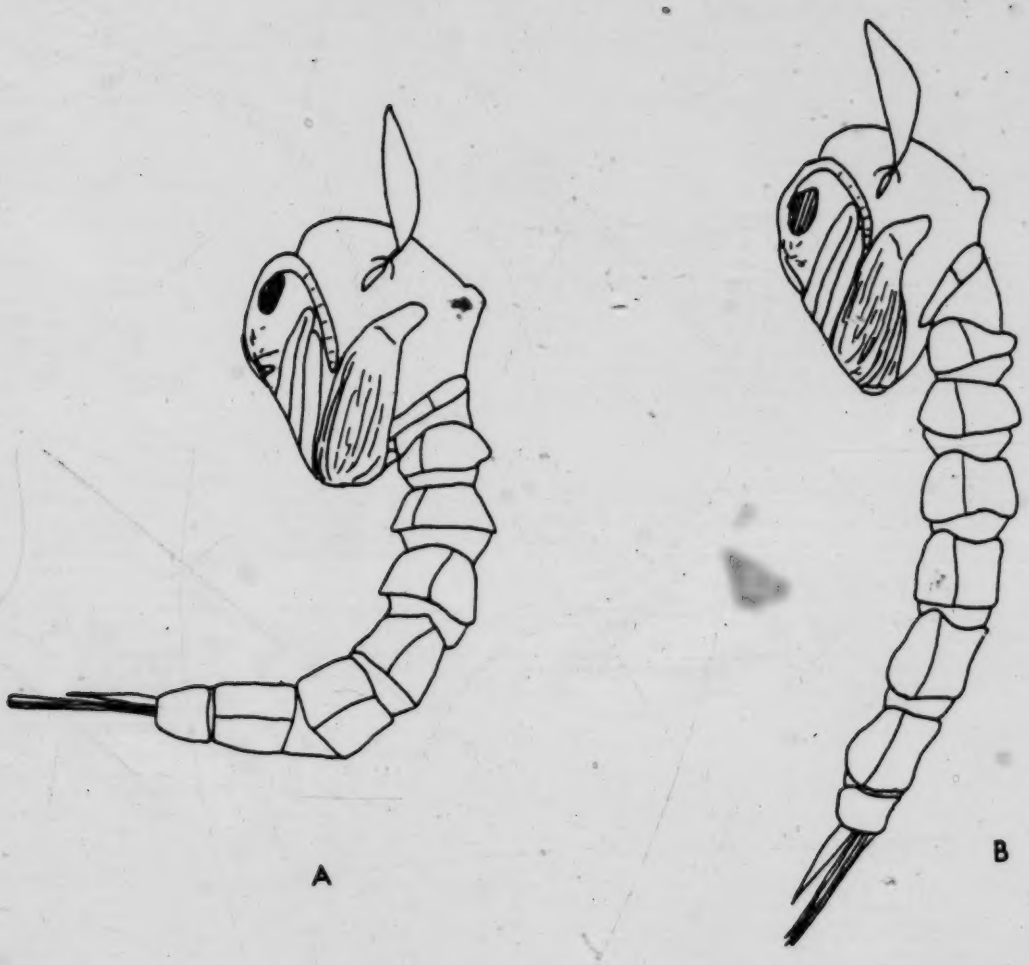


Figure 5. Posture of live pupae. A. Chaoborus cooki. B. Chaoborus trivittatus. Drawings from photographs of live pupae.

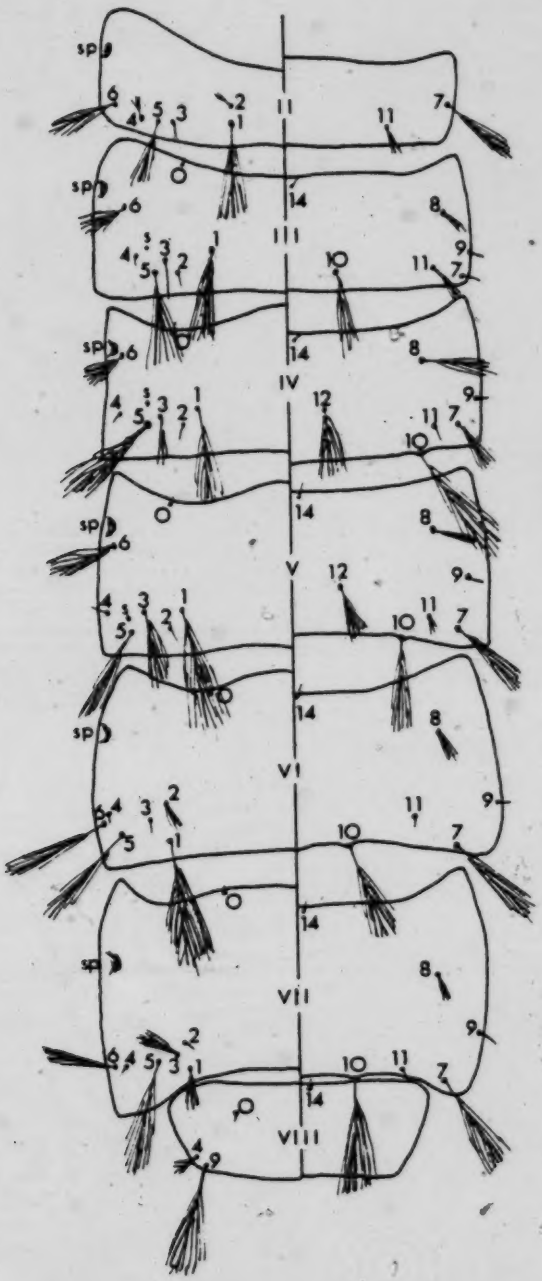


Figure 6. Abdominal chaetotaxy of pupa of Schadonophasma. Setae numbered after Belkin et al. (1970). S: sensilla; sp: spiracular scar.

Figure 7. Antenna and dorsal outline of head capsule of larval instars of Schadonophasma. Antennae: A. First instar; B. Second instar; C. Third instar; D. Fourth instar. Dorsal outline of head capsule: E. First instar of Chaoborus cooki; F. First instar of Chaoborus trivittatus; G. Second instar; H. Third instar; I. Fourth instar. J. Egg burster of first instar of C. cooki. K. Egg burster of first instar of C. trivittatus.

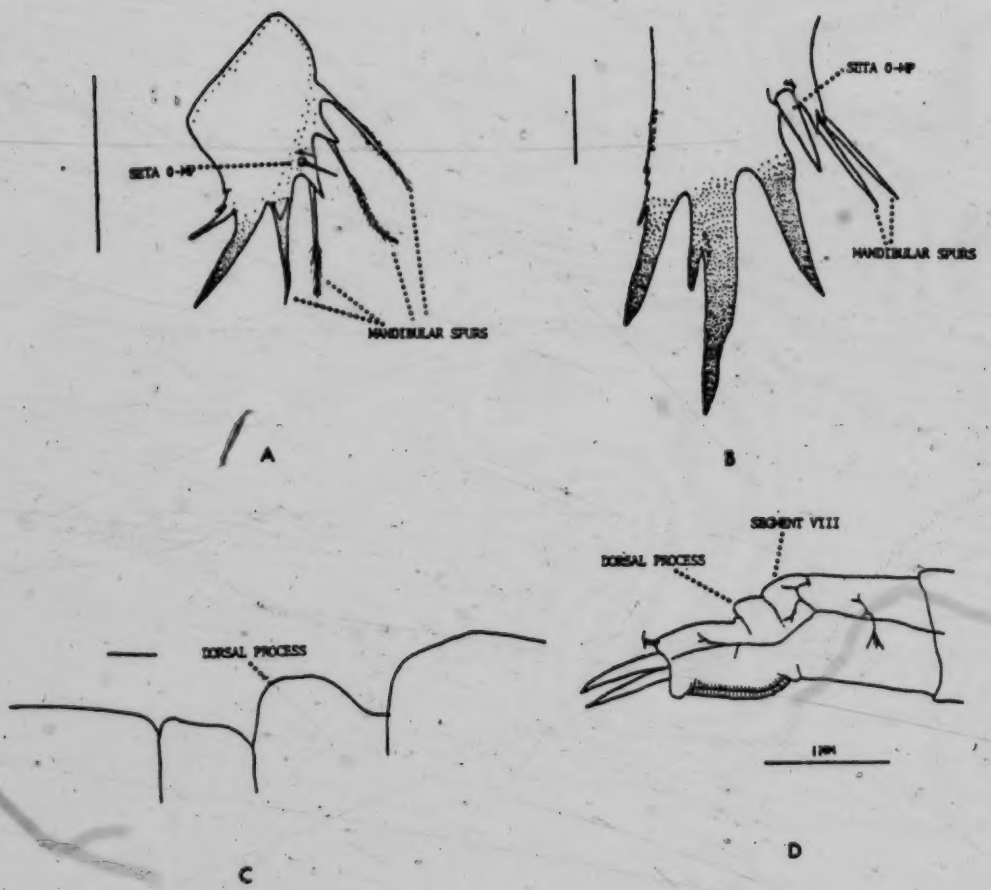


Figure 8. A. Mandible of first instar larva B. Mandible of fourth instar larva. C. Dorsal process of fourth instar larva of Chaoborus nylaei. D. Terminal abdominal segments of fourth instar larva of Chaoborus cooki showing position of tracheae.

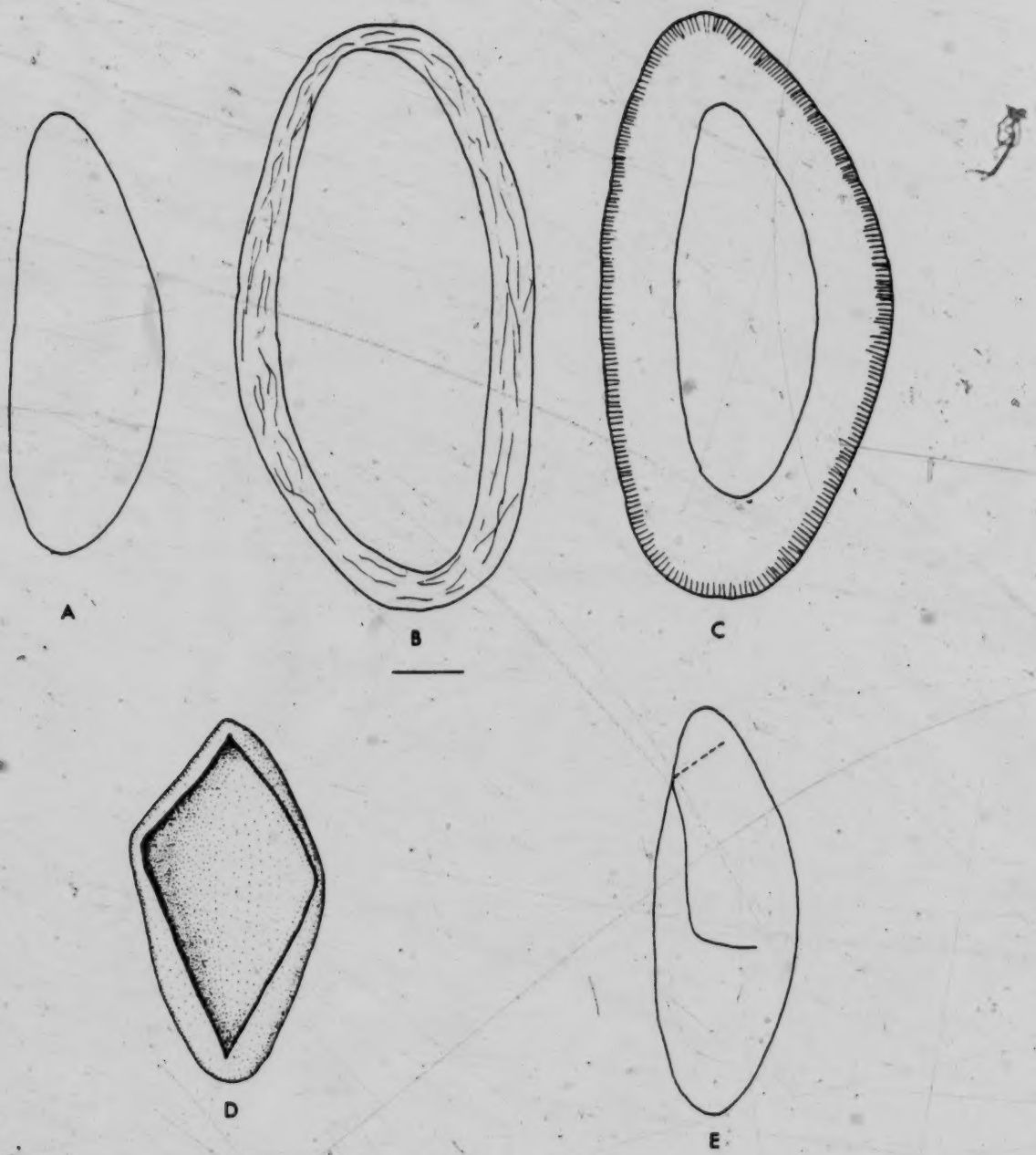


Figure 9. Egg structure. A. Chaoborus trivittatus. B. Chaoborus nyblaei. C. Chaoborus cooki. Egg shell. D. Chaoborus trivittatus. E. Chaoborus cooki (fracture line indicated).

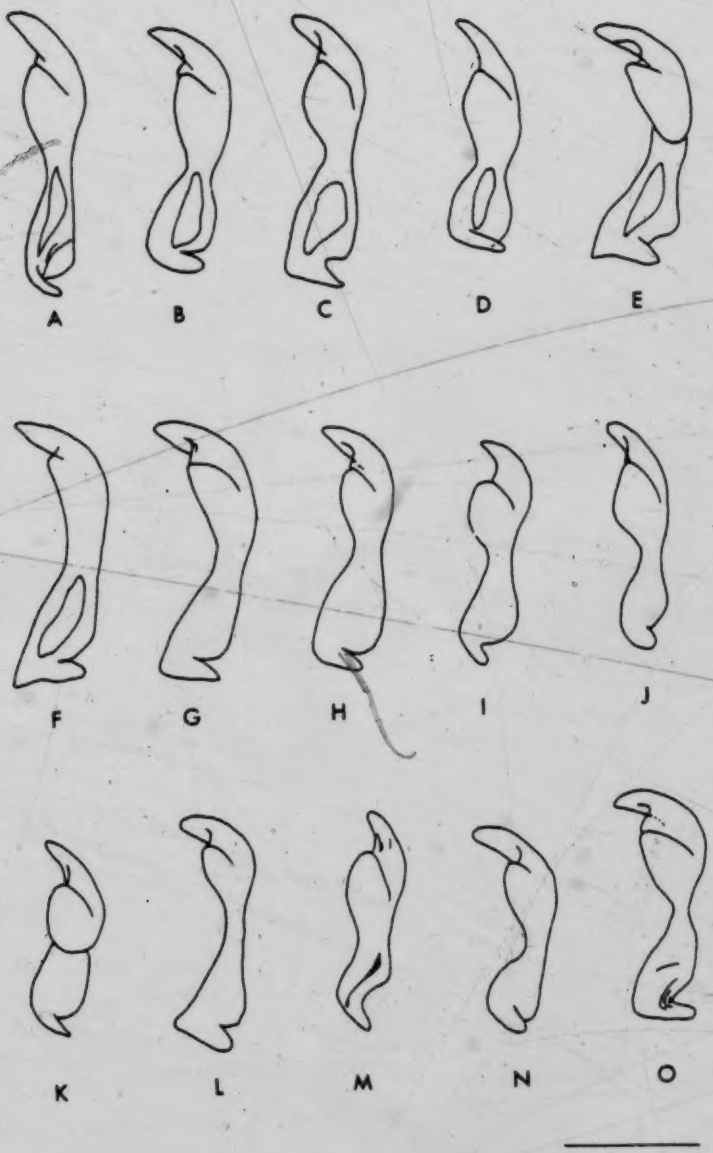


Figure 10. Penis valves of adult male Chaoborus trivittatus. A-G. Intrapopulational variation of specimens from 2.4 km. west of Edmonton, Alberta. H-O. Interpopulational variation of specimens from: H. Banff, Alberta; I. Hoodsport, Washington; J. North Burgess Twp., Ontario; K. Whitehorse, Yukon Territory; L. Old Chelsea, Ontario; M. Lake 241, Kenora, Ontario (holotype of C. brunskilli); N. Stanford, California; H. Maine (holotype of C. trivittatus).

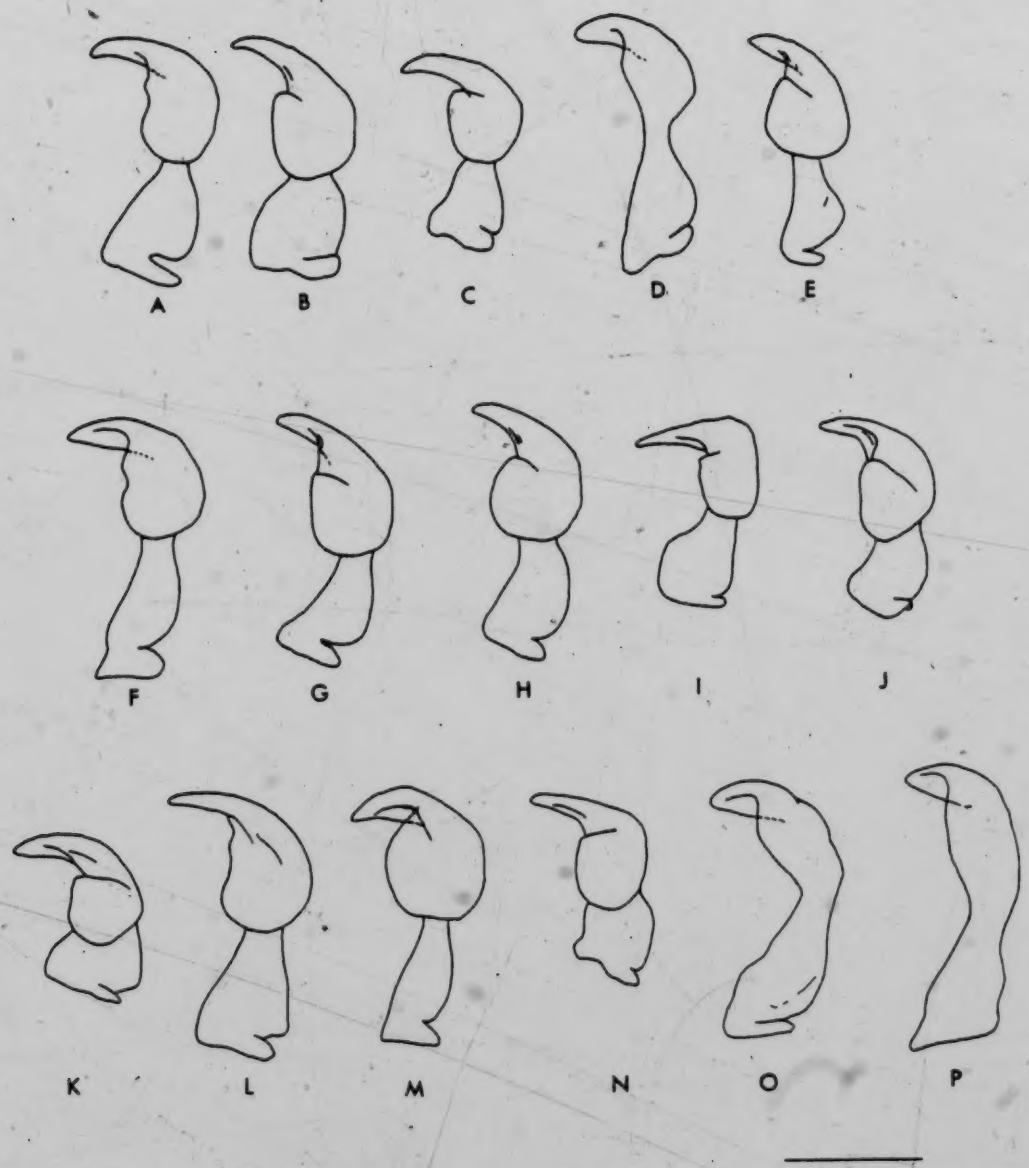


Figure 11. Penis valves of adult male Chaoborus cooki. A-H. Intrapopulational variation of specimens from 1.4 km. west of George Lake, Alberta. I-N. Interpopulational variation of specimens from: I. Km. 140, Dempster Highway, Yukon Territory; J. Churchill, Manitoba; K. Gillam, Manitoba; L. Whitehorse, Yukon Territory; M. Yellowknife, Northwest Territories; N. Chisholm, Ontario. Penis valves of adult male Chaoborus nyblaei. Specimens from: O. 2-3 km. SW Nuorgam, Finland; P. Abisko, Sweden.

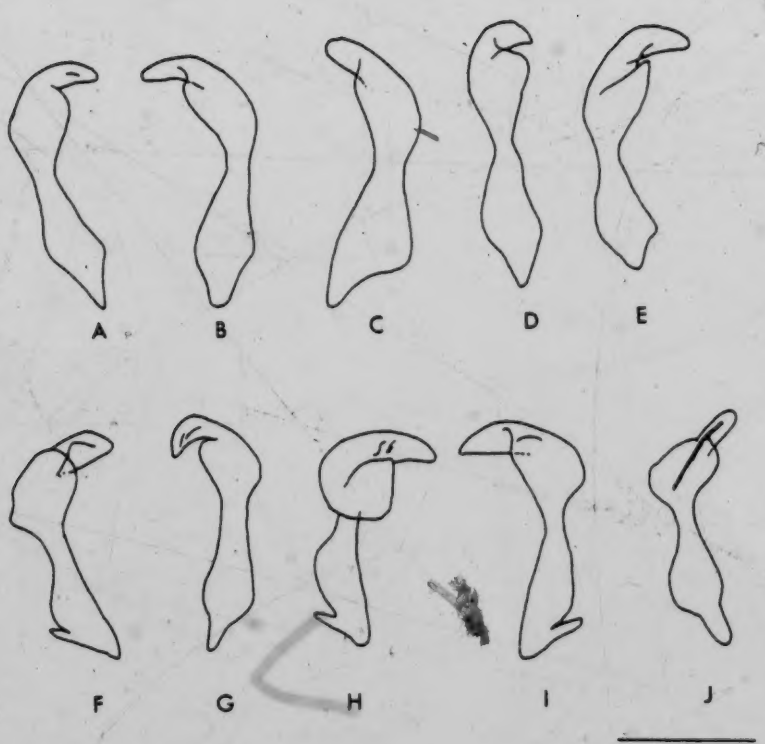


Figure 12. Variation of penis valves of adult males due to orientation.
A-E. Chaoborus trivittatus from 1.6 km. west of Edmonton, Alberta.
F-J. Chaoborus cooki from 32 km. west of Edson, Alberta.

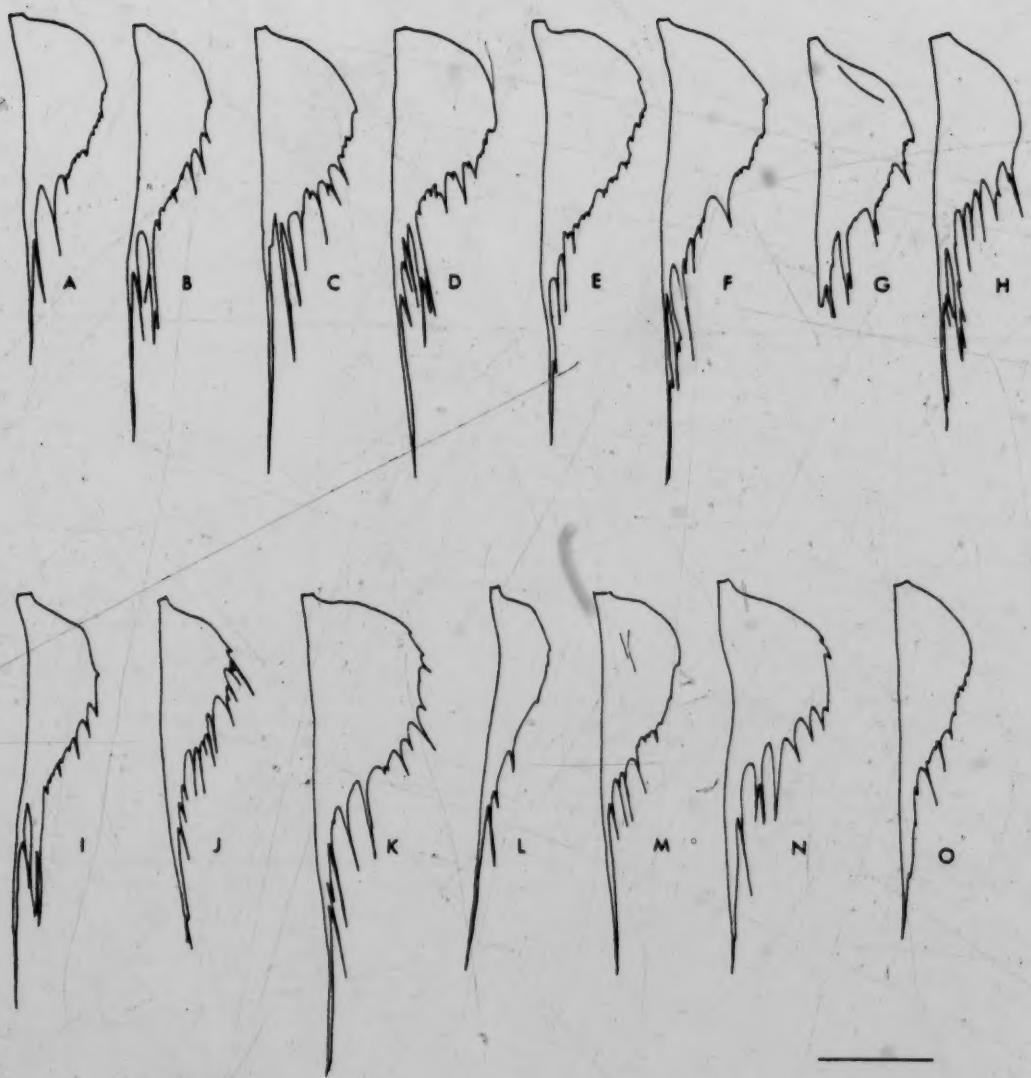


Figure 13. Prelabral appendages of fourth instar larvae of Chaoborus trivittatus. A-G. Intrapopulational variation of specimens from 2.4 km. west of Edmonton, Alberta. H-O. Interpopulational variation of specimens from: H. 4.8 km. north of St. John's, Newfoundland; I. 2.4 km. west of Edmonton, Alberta; J. 2.4 km. south of Robb, Alberta; K. Gwendoline Lake, British Columbia; L. 4.8 km. east of Sicamous, British Columbia; M. 45 km. east of Jasper, Alberta; N. Lake 241, Kenora, Ontario; O. East Henry Pond, Jasper National Park, Alberta.

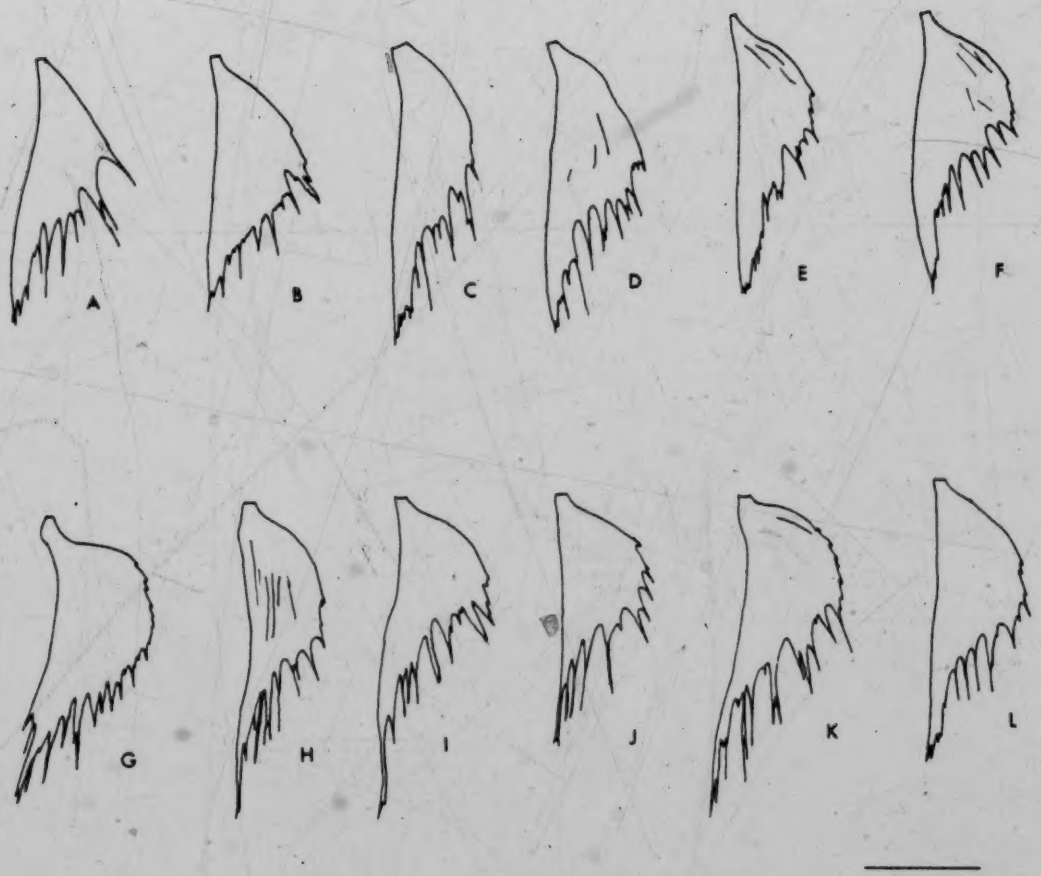


Figure 14. Prelabral appendages of fourth instar larvae of Chaoborus cooki. A-F. Intrapopulational variation of specimens from 1.6 km. south of Jasper, Alberta. G-L. Interpopulational variation of specimens from: G. Churchill, Manitoba; H. Pond nr. Harris River, Northwest Territories; I. Dempster Highway, Yukon Territory; J. 1.4 km. west of George Lake, Alberta; K. Klutlane Glacier moraine, Yukon Territory; L. 23.3 km. west of Jasper, Alberta.

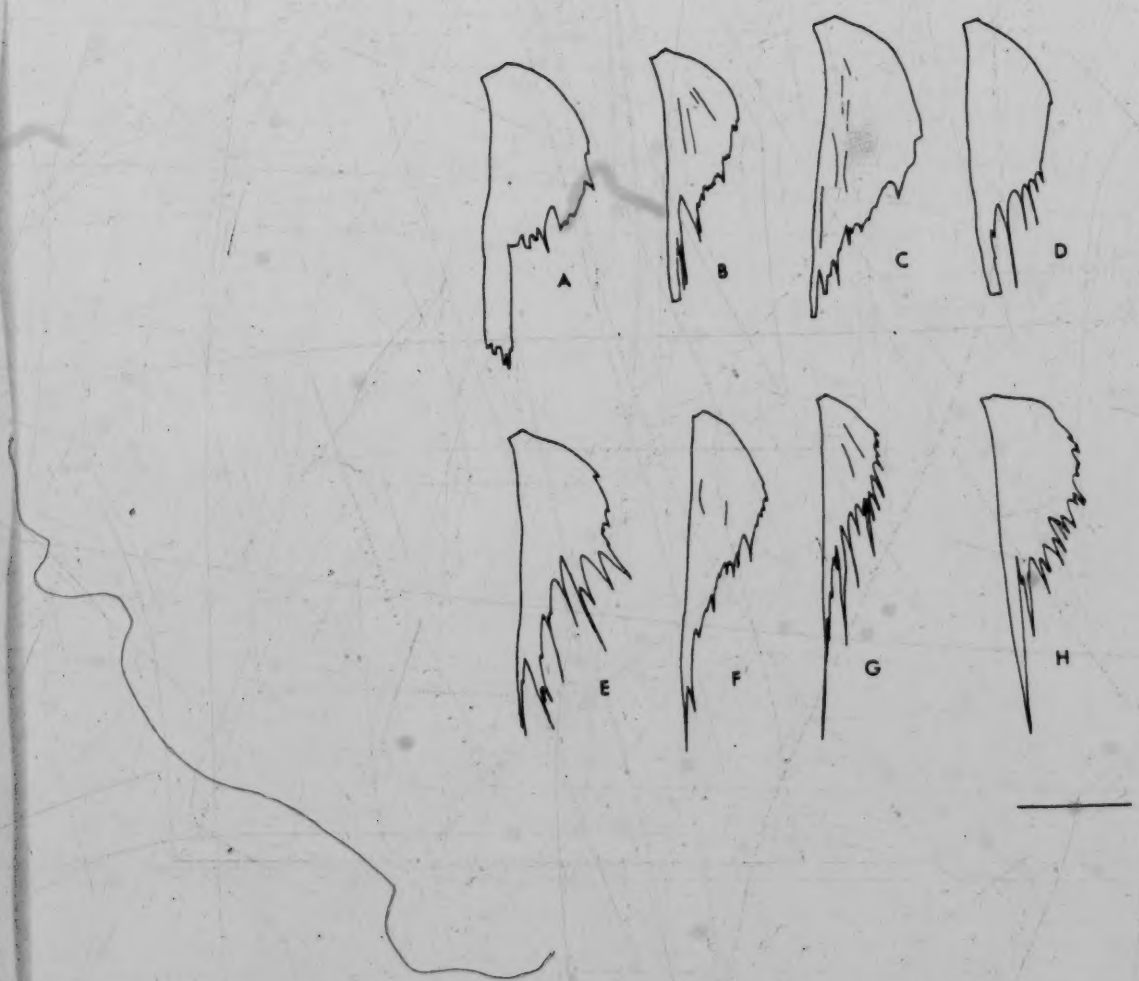


Figure 15. Prelabral appendages of fourth instar larvae of Chaoborus nyblaei from 2-3 km. southwest of Nuorgam, Finland.

Figure 16. Known distribution of Chaoborus trivittatus.

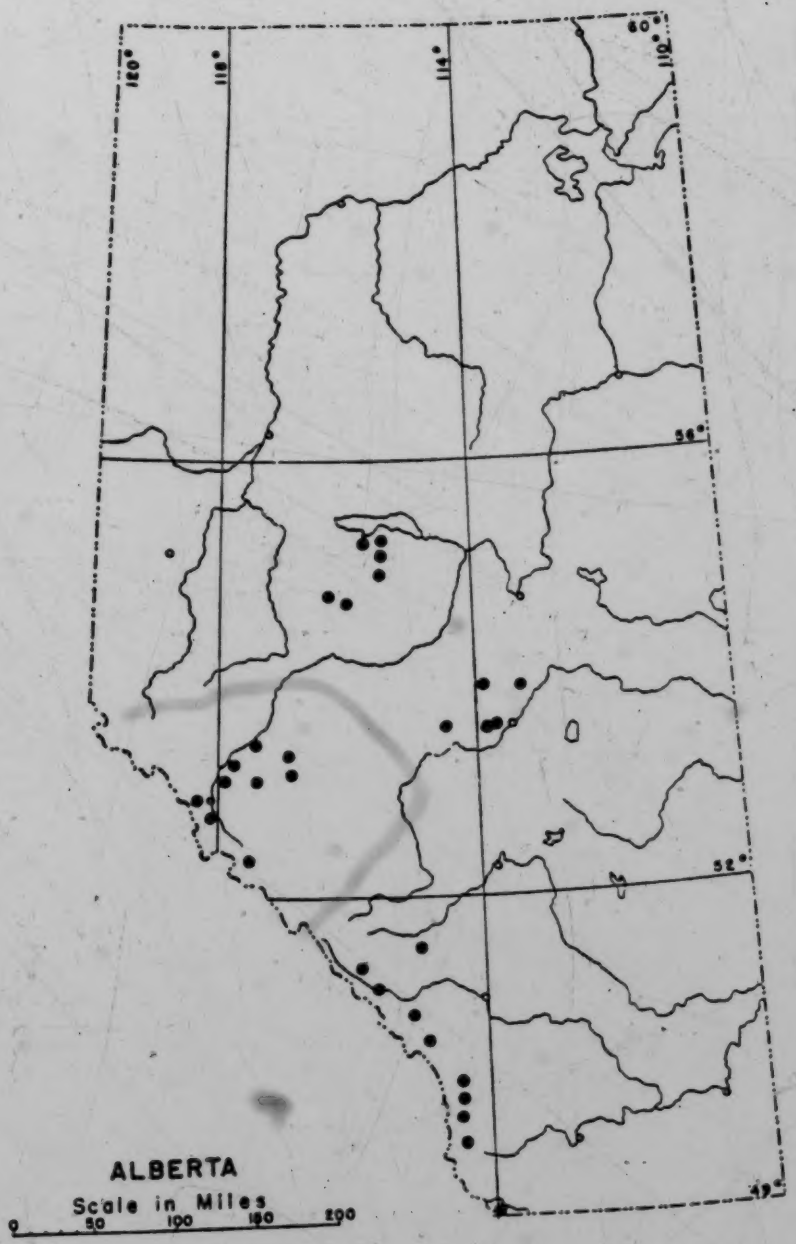


Figure 17. Known distribution of Chaoborus trivittatus in Alberta.

Figure 18. Known distribution of Chaoborus cooki.

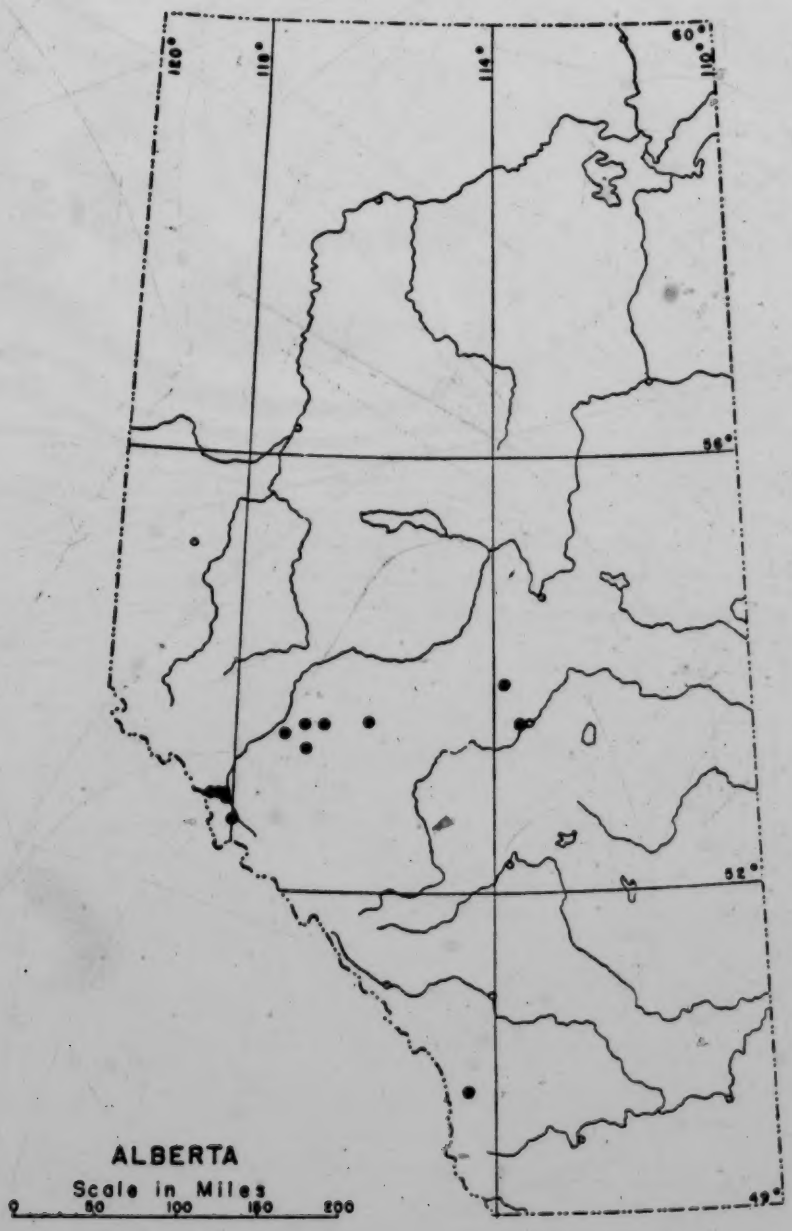
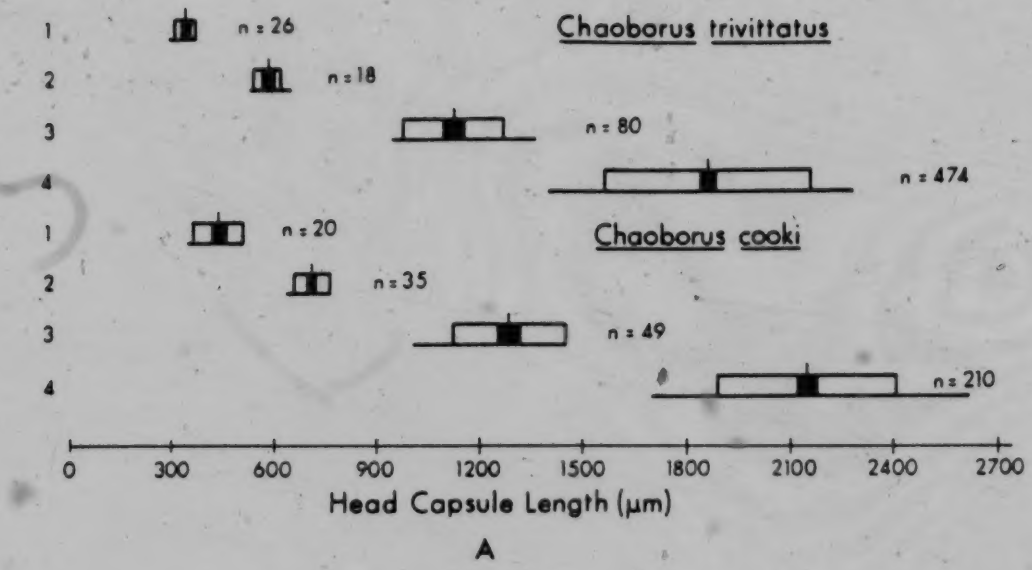


Figure 19. Known distribution of Chaoborus cooki in Alberta.

Figure 20. Known distribution of Chaoborus nyblaei.



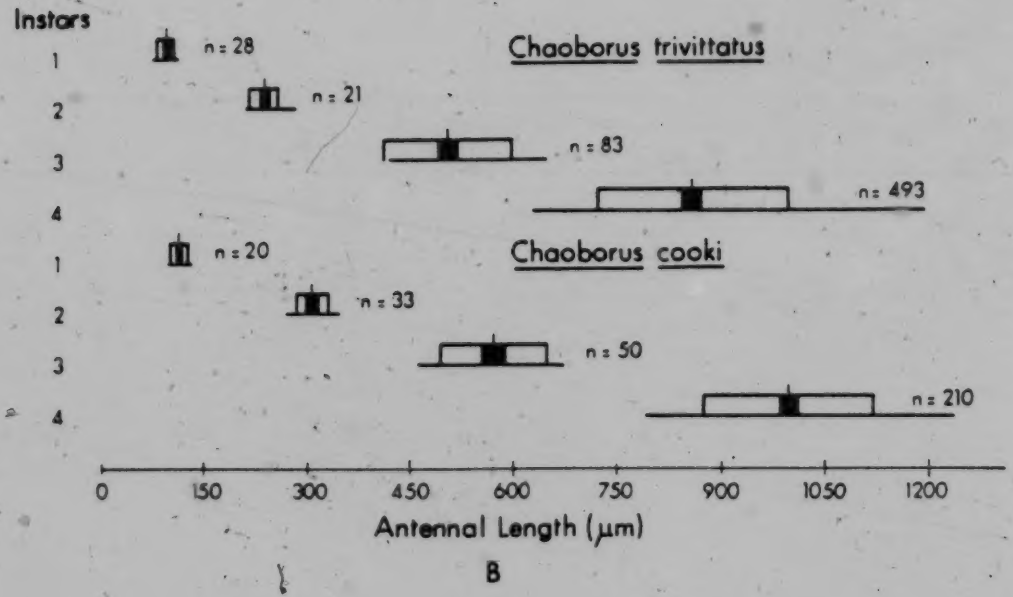
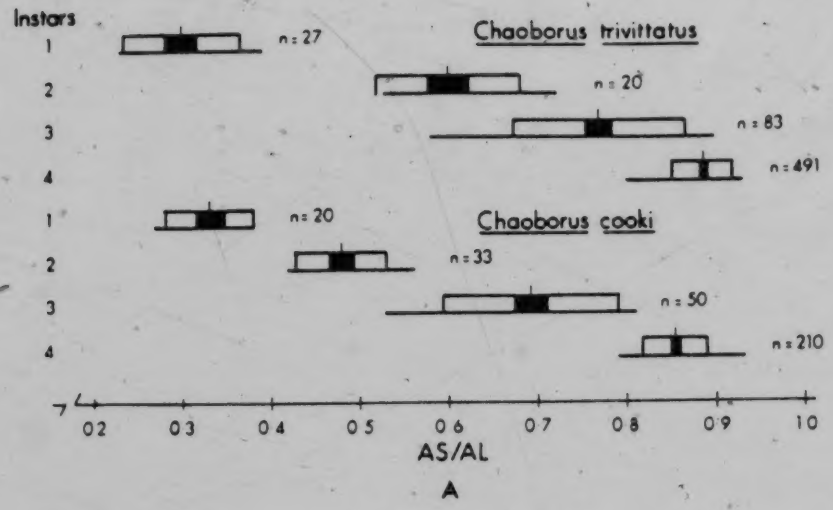


Figure 21. Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. Head capsule length. B. Antennal length.



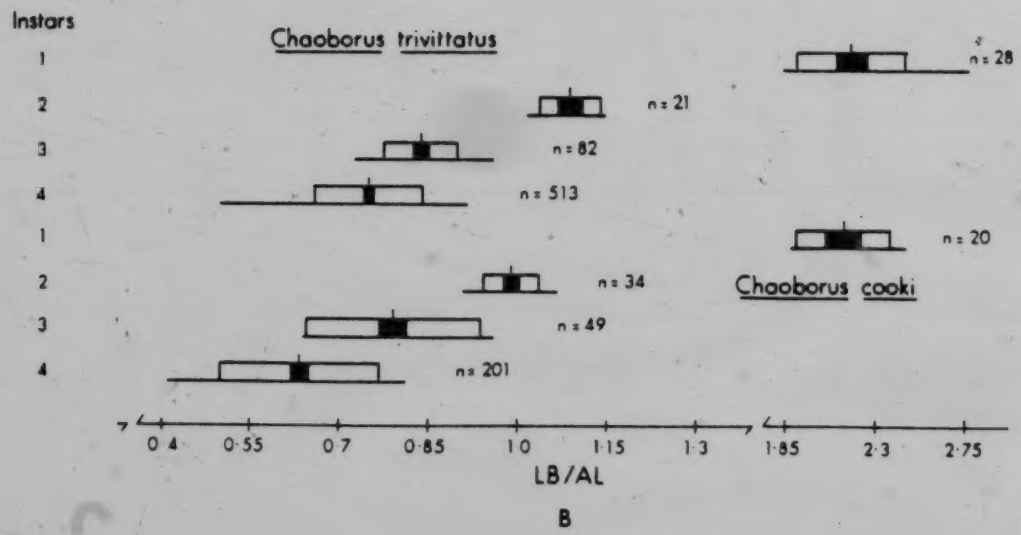


Figure 22. Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. AS/AL. B. LB/AL.

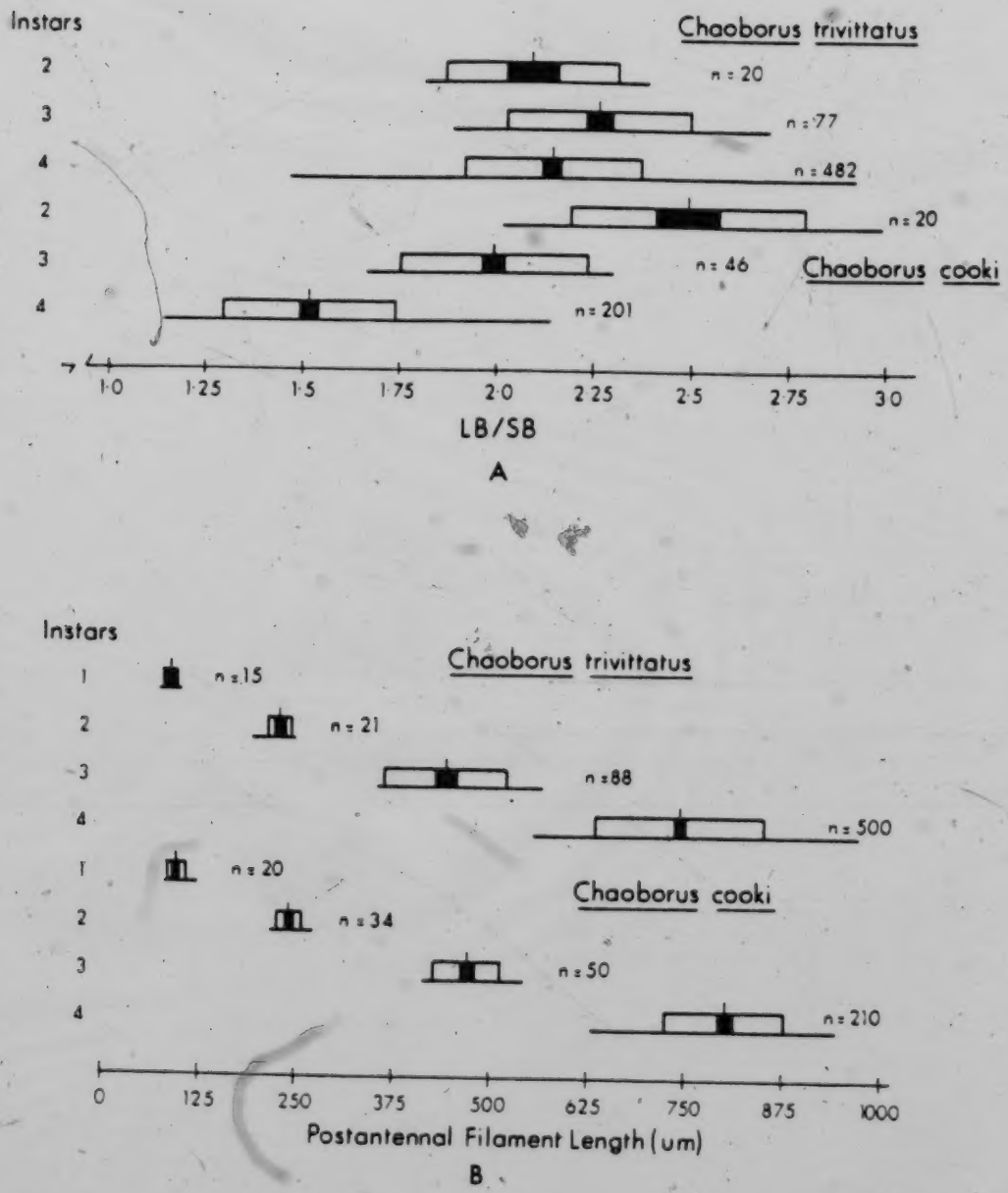
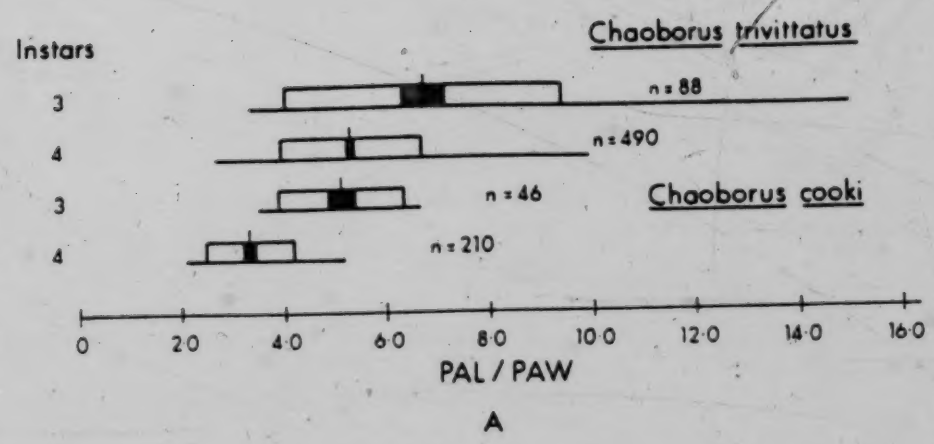


Figure 23. Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. LB/SB. B. Postantennal filament length.



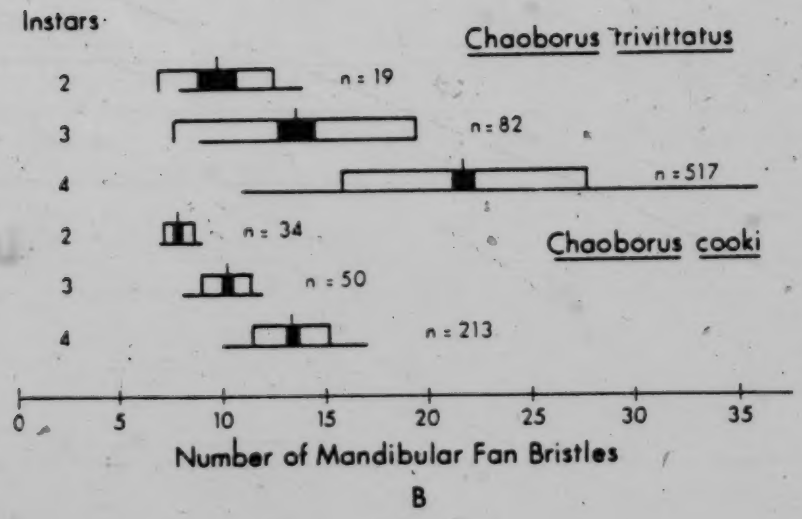


Figure 24. Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. PAL/PAW. B. Number of mandibular fan bristles.

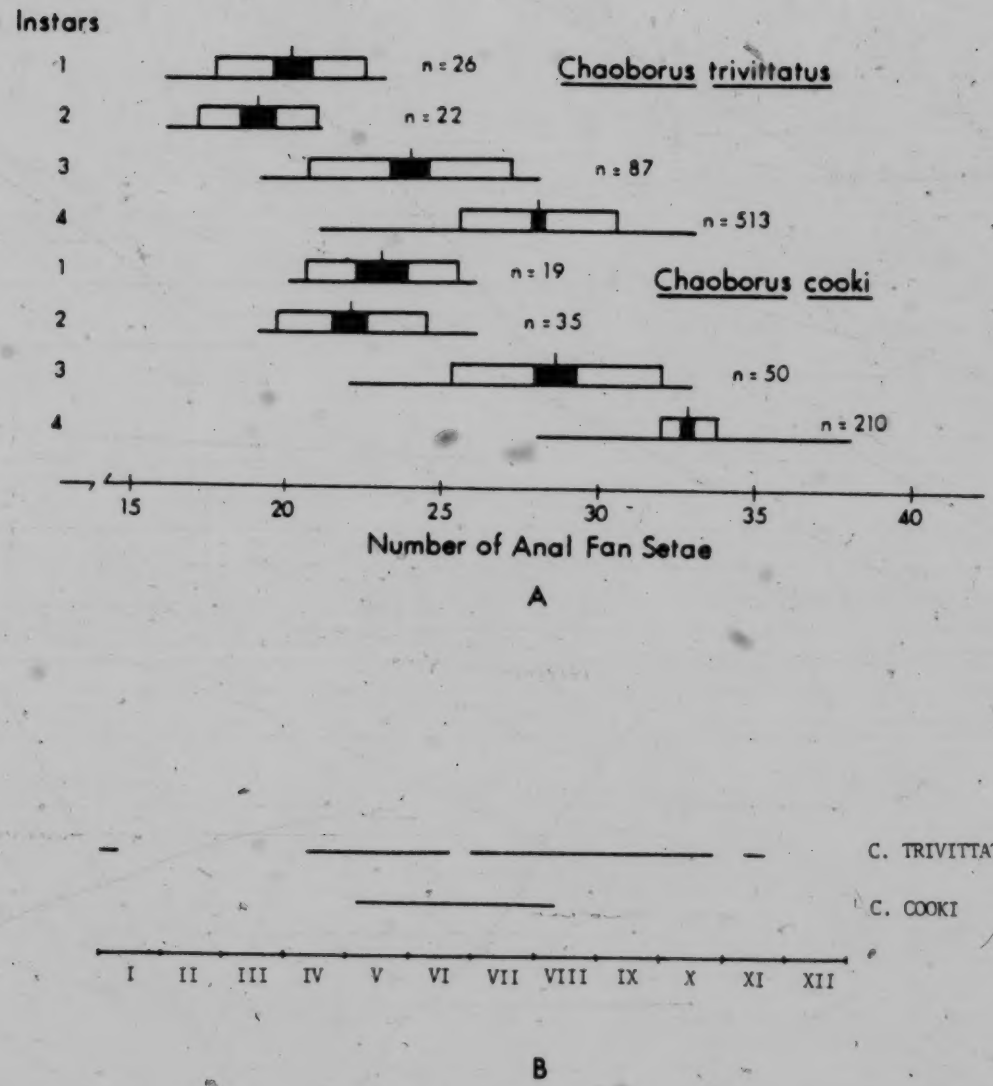


Figure 25. Variation of characters of larval instars of Chaoborus trivittatus and Chaoborus cooki. A. Number of anal fan setae. B. Temporal distribution of fourth instar larvae of Chaoborus trivittatus and Chaoborus cooki.

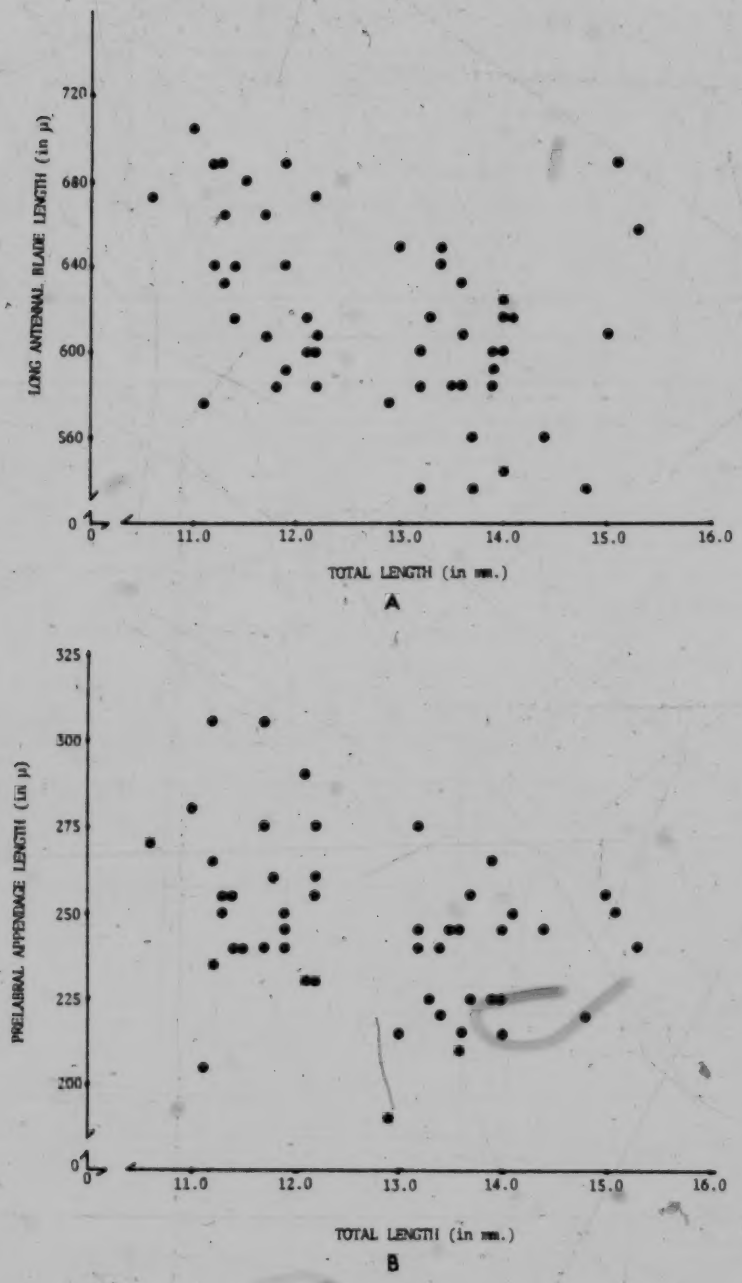


Figure 26. Age-related variation of male fourth instar larvae of Chaoborus cooki. A. Relationship between total length and long antennal blade length. B. Relationship between total length and prelabral appendage length.

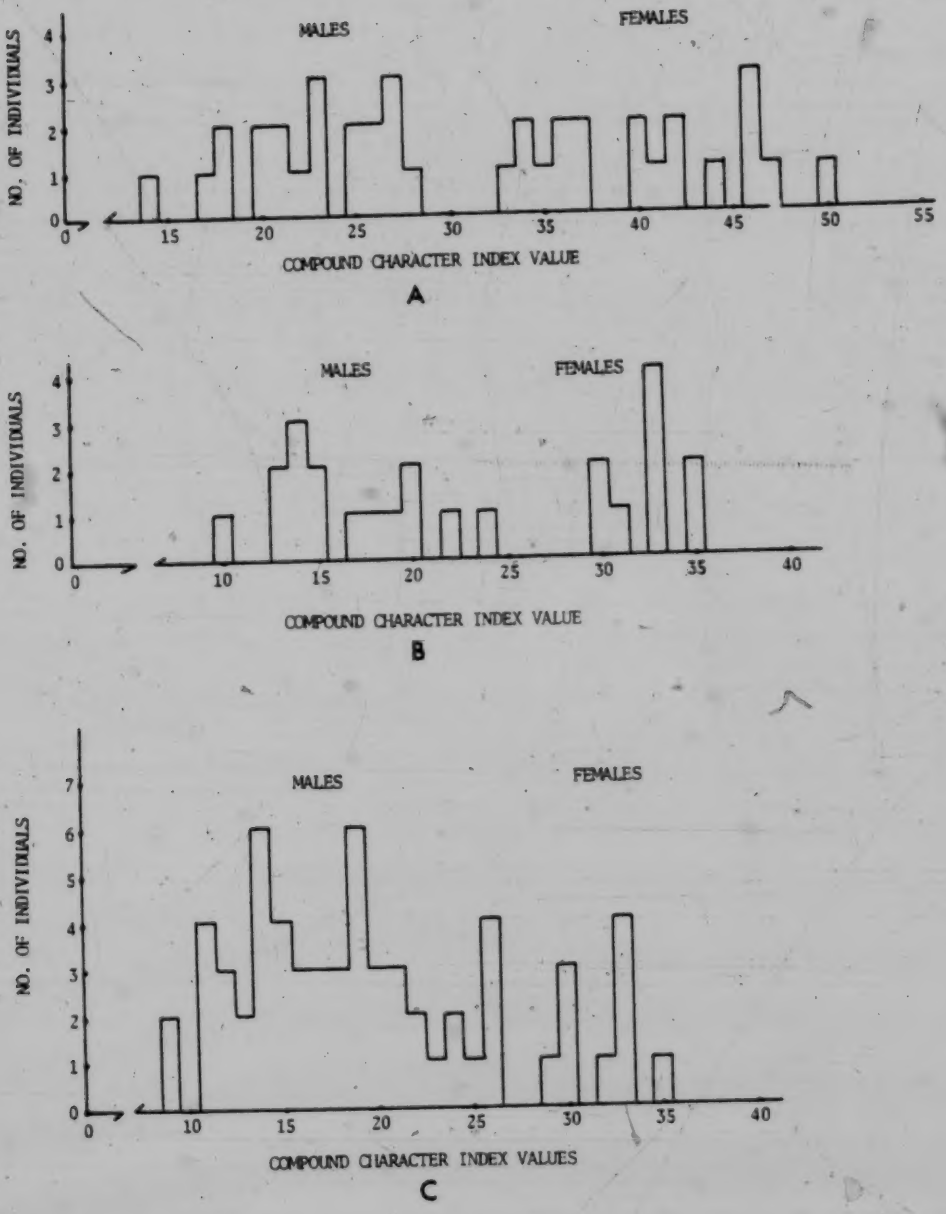


Figure 27. Results of compound character index used to sex fourth instar larvae. A. Of Chaoborus trivittatus from 2.4 km. west of Edmonton, Alberta. B. Of Chaoborus cooki from 32 km. west of Edson, Alberta. C. Of Chaoborus cooki from 1.6 km. south of Jasper, Alberta.

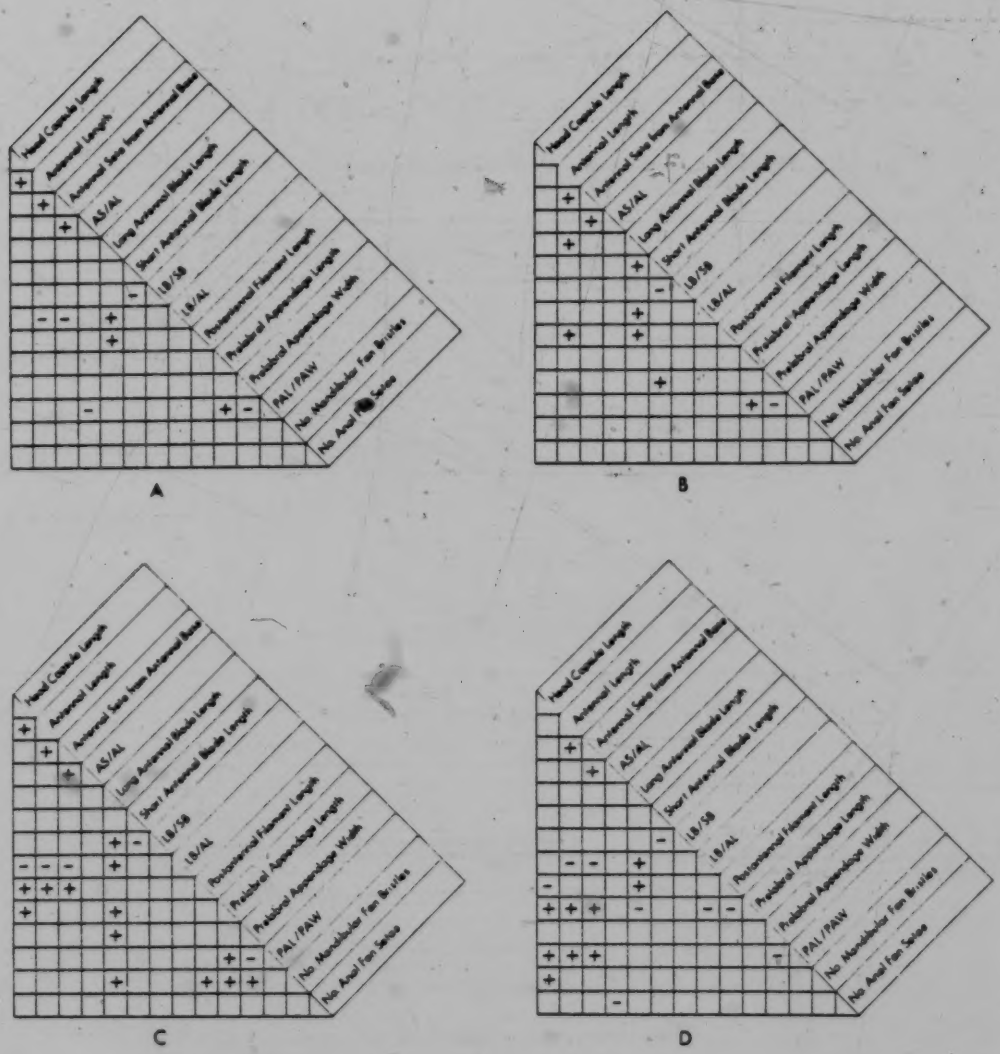


Figure 28. Correlation of characters of fourth instar larvae. A. Male Chaoborus trivittatus. B. Female C. trivittatus. C. Male Chaoborus cooki. D. Female Chaoborus cooki. Open spaces represent lack of significant correlation; + and - signify positively and negatively significant correlations, respectively.

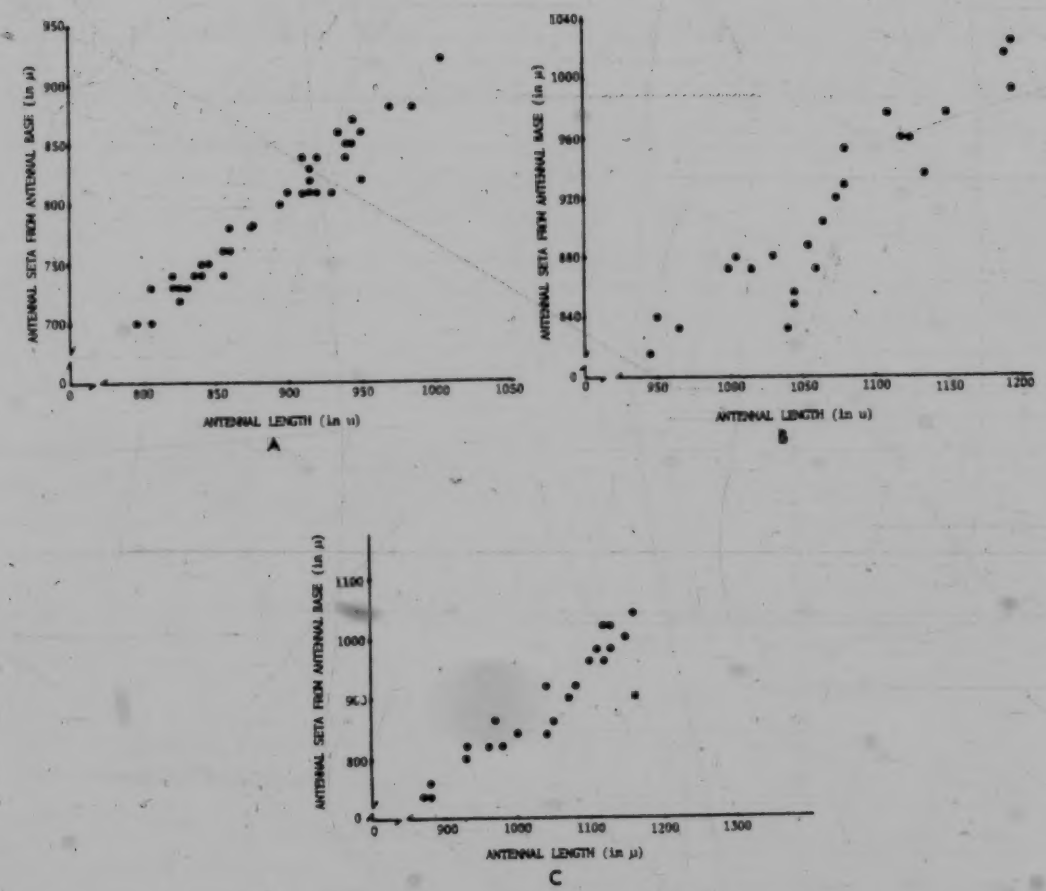

ANTENNAL SETA FROM ANTENNAL BASE (in μ)
ANTENNAL LENGTH (in μ)
A
ANTENNAL SETA FROM ANTENNAL BASE (in μ)
ANTENNAL LENGTH (in μ)
B
ANTENNAL SETA FROM ANTENNAL BASE (in μ)
ANTENNAL LENGTH (in μ)
C

Figure 29. Relationship between antennal length and distance of antennal seta from base of antenna of fourth instar larvae. A. Chaoborus trivittatus. B. Chaoborus cooki. C. Chaoborus nyblaei.

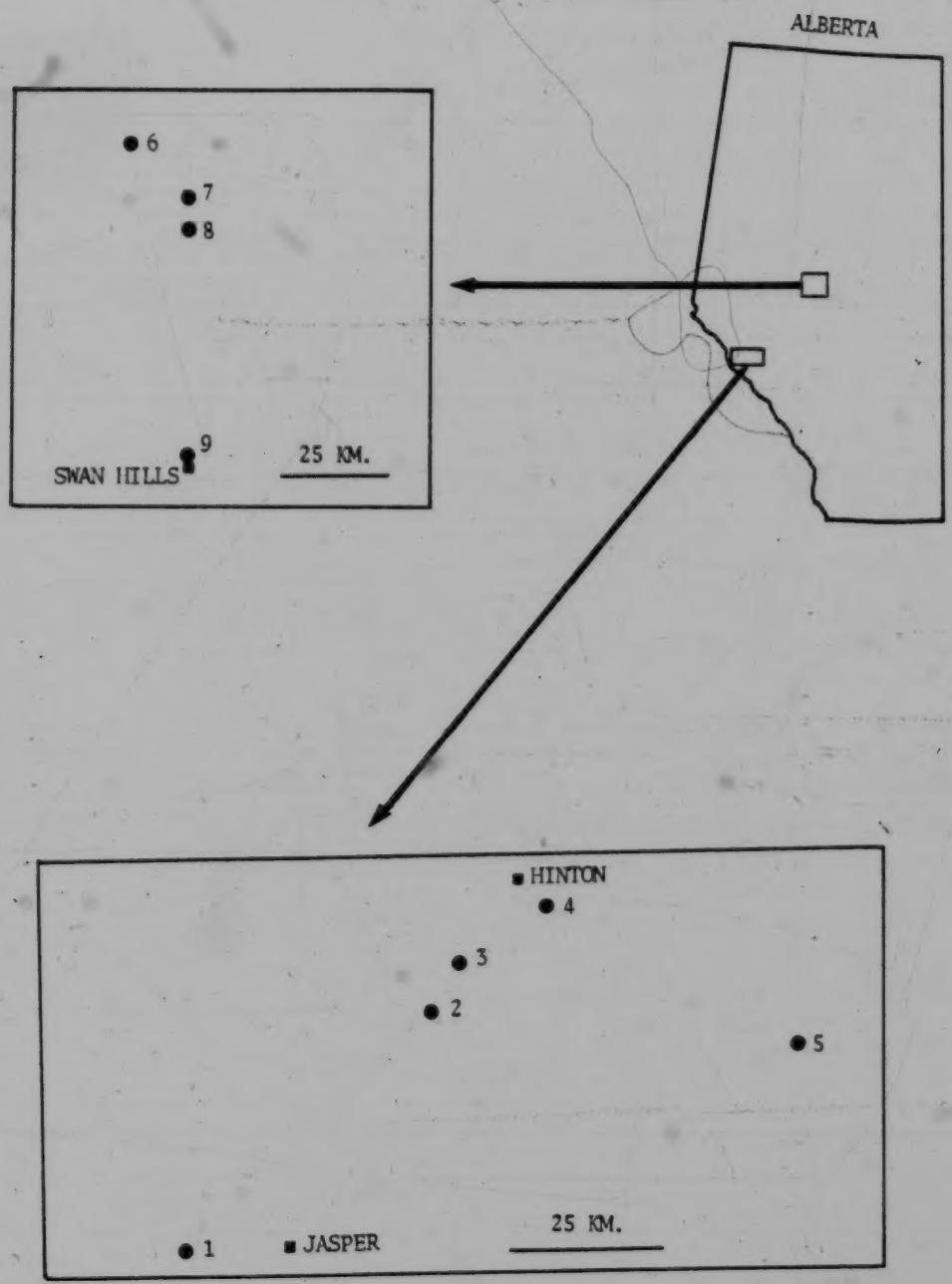


Figure 30. Localities of samples used to study geographical variation of characters of fourth instar larvae of Chaoborus trivittatus in Alberta. Samples from: 1. 16 km. west of Jasper; 2. 45 km. east of Jasper; 3. Pond nr. Kinky Lake; 4. 4.8 km. south of Hinton; 5. 2.4 km. south of Robb; 6. 69 km. east of High Prairie; 7. 61 km. north of Swan Hills; 8. 53 km. north of Swan Hills; 9. 1.6 km. north of Swan Hills.

Figure 31. Localities of samples used to study geographical variation of characters of fourth instar larvae of Chaoborus trivittatus from the west coast of North America. Samples from: 1. Klutlane Glacier moraine, Yukon Territory; 2. Prince Rupert, British Columbia; 3. Gwendoline Lake, British Columbia; 4. Eunice Lake, British Columbia; 5. Hall Lake, Washington; 6. Mad River, California; 7. Stanford and Jewel Lake, California.

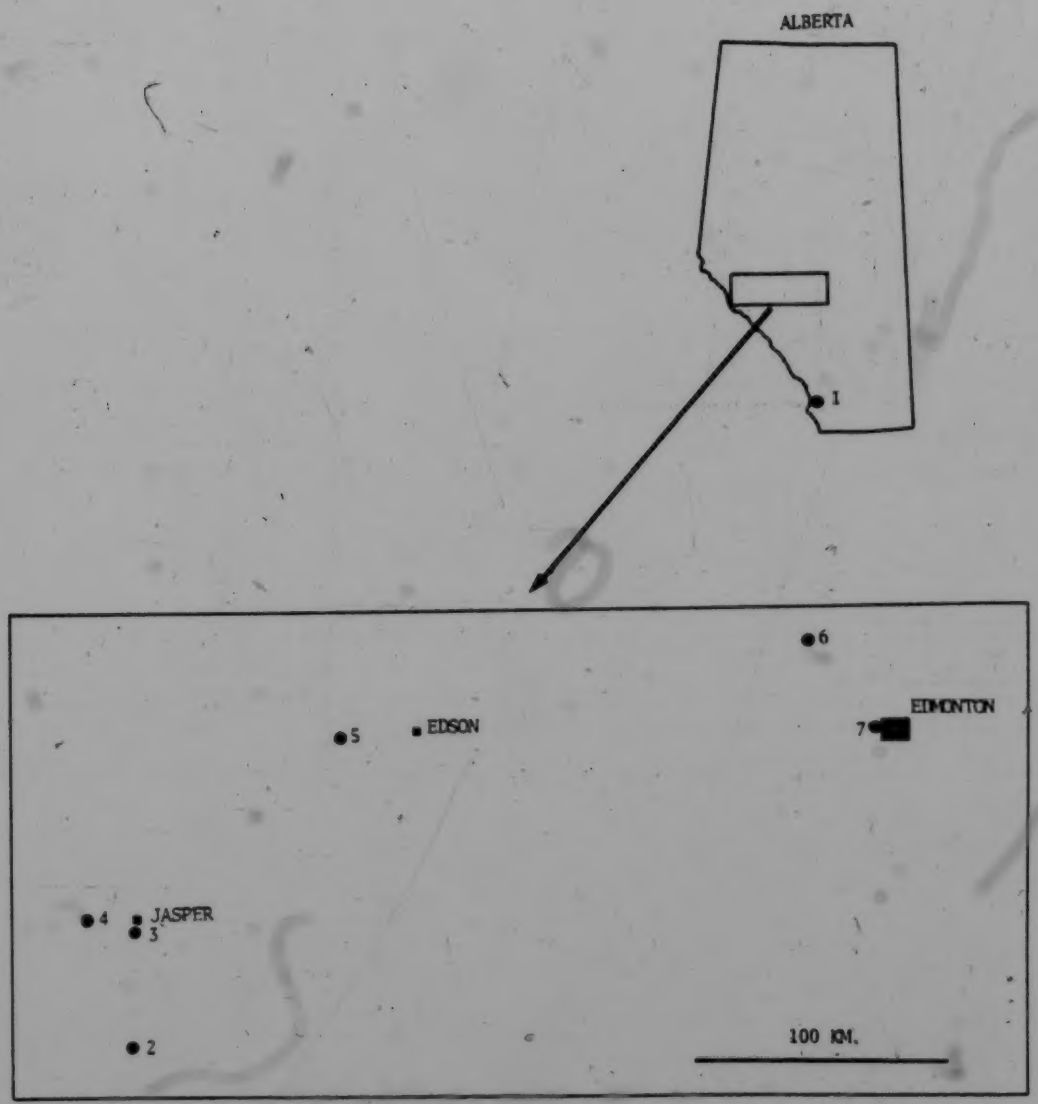


Figure 32. Localities of samples used to study geographical variation of characters of fourth instar larvae of Chaoborus cooki in Alberta. Samples from: 1. 69 km. north of Coleman; 2. 53 km. south of Jasper; 3. 1.6 km. south of Jasper; 4. 6.4 and 23.3 km. west of Jasper; 5. 32 km. west of Edson; 6. 1.4 km. west of George Lake; 7. 2.4 km. west of Edmonton.

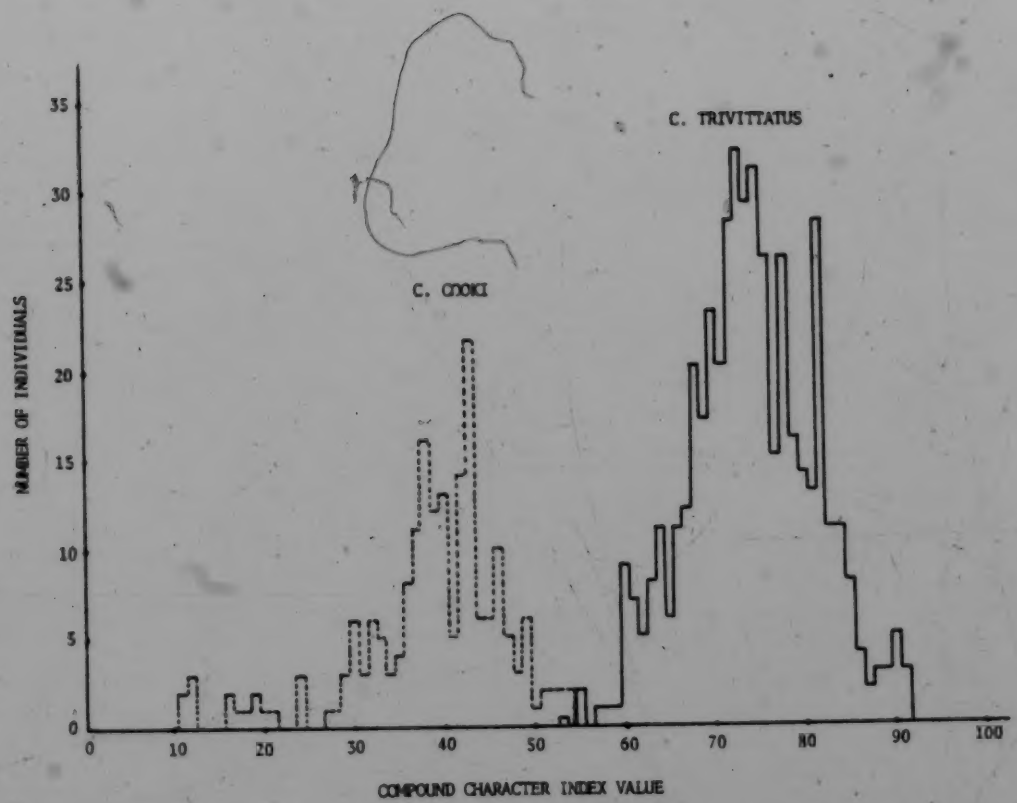


Figure 33. Results of compound character index used to recognize fourth instar larvae of Chaoborus trivittatus and Chaoborus cooki.

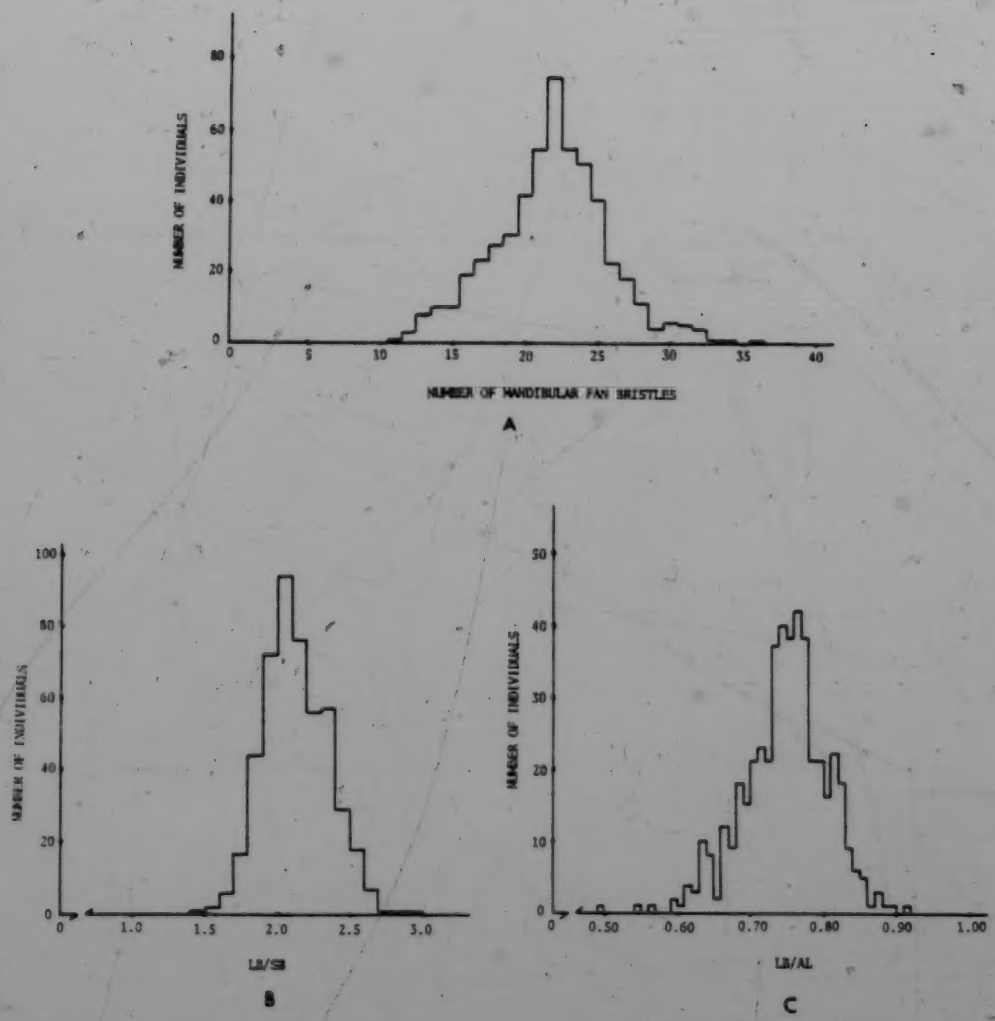


Figure 34. Variation of characters of fourth instar larvae of Chaoborus trivittatus. A. Number of mandibular fan bristles. B. LB/SB. C. LB/AL.

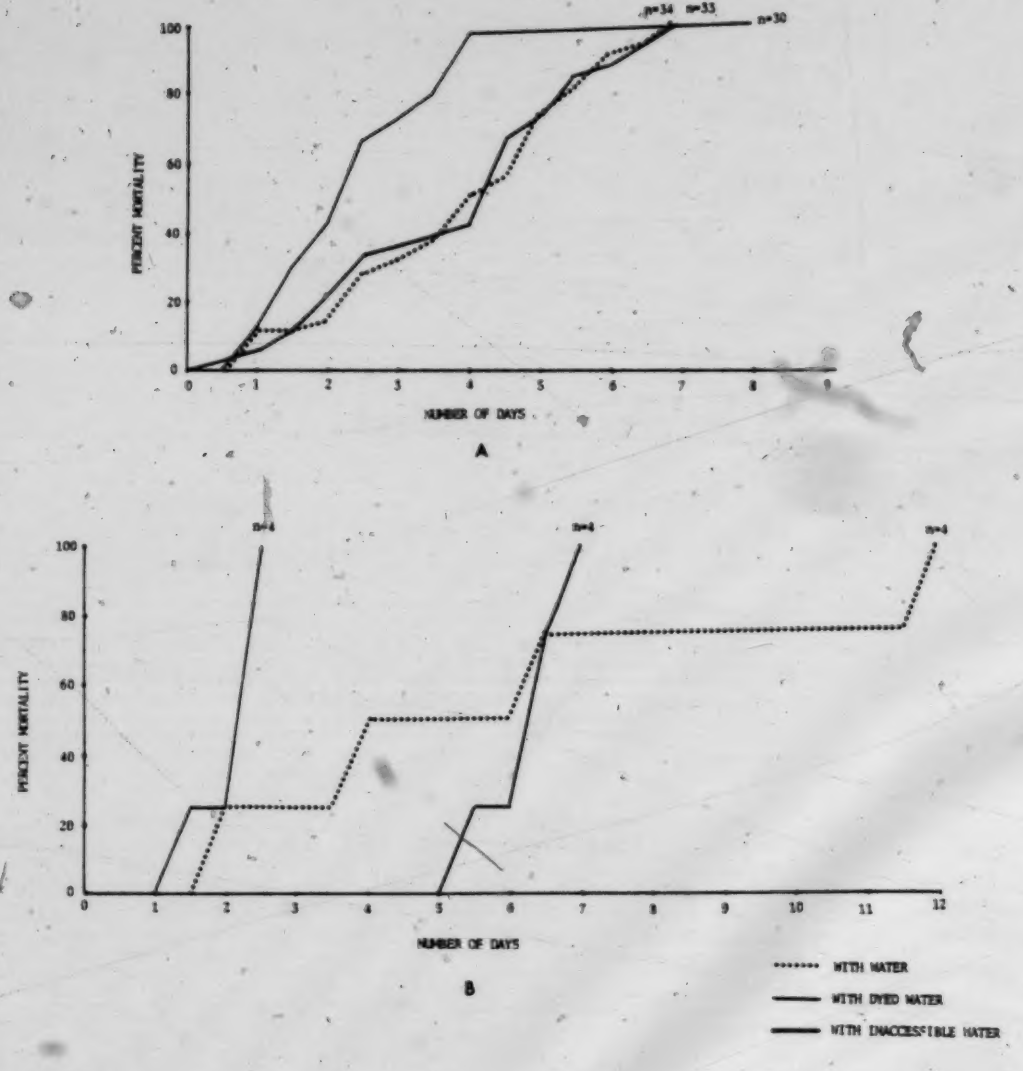


Figure 35. Mortality of adult Chaoborus trivittatus. A. Males. B. Females.

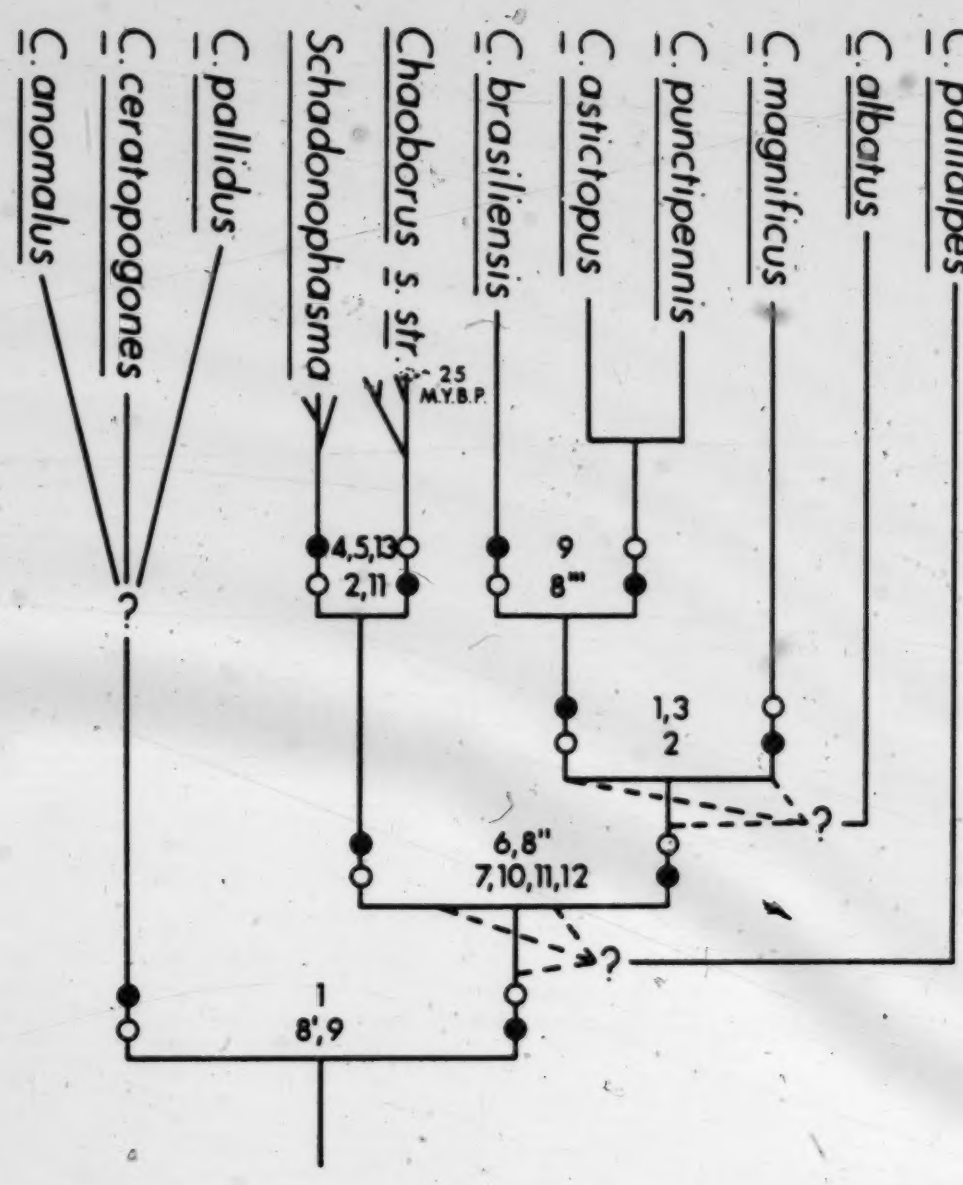


Figure 36. Phylogeny of species of Chaoborus. Black circles signify apomorphic states, open circles plesiomorphic states. M.Y.B.P. indicates million years before present.

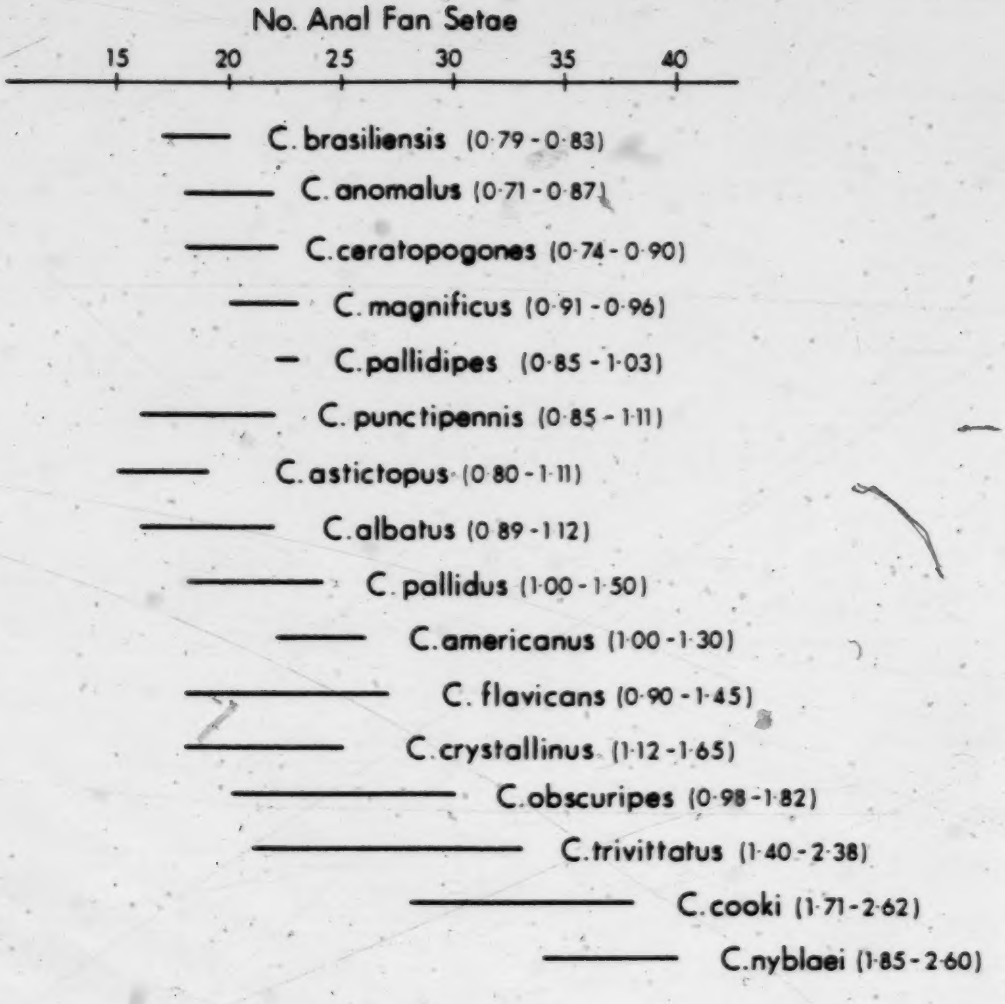


Figure 37. Relationship between number of anal fan setae and head capsule length (given in parentheses as mm.) of fourth instar larvae of Chaoborus species.

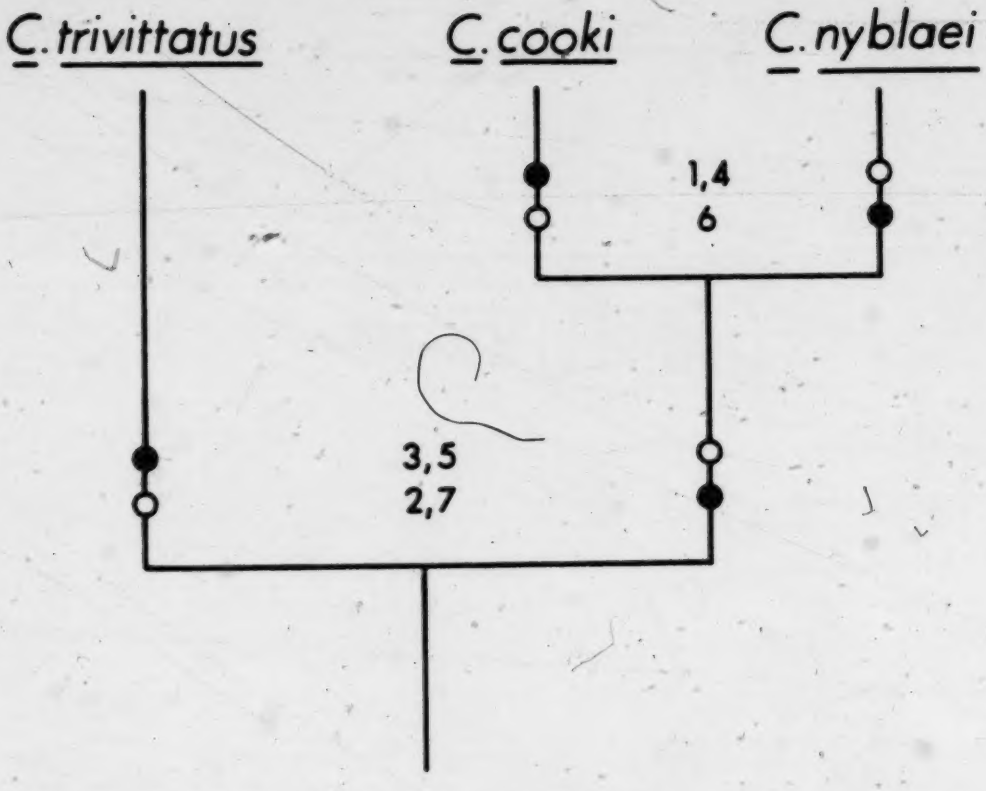


Figure 38. Phylogeny of species of Schadonophasma. Black circles signify apomorphic states, open circles plesiomorphic states.

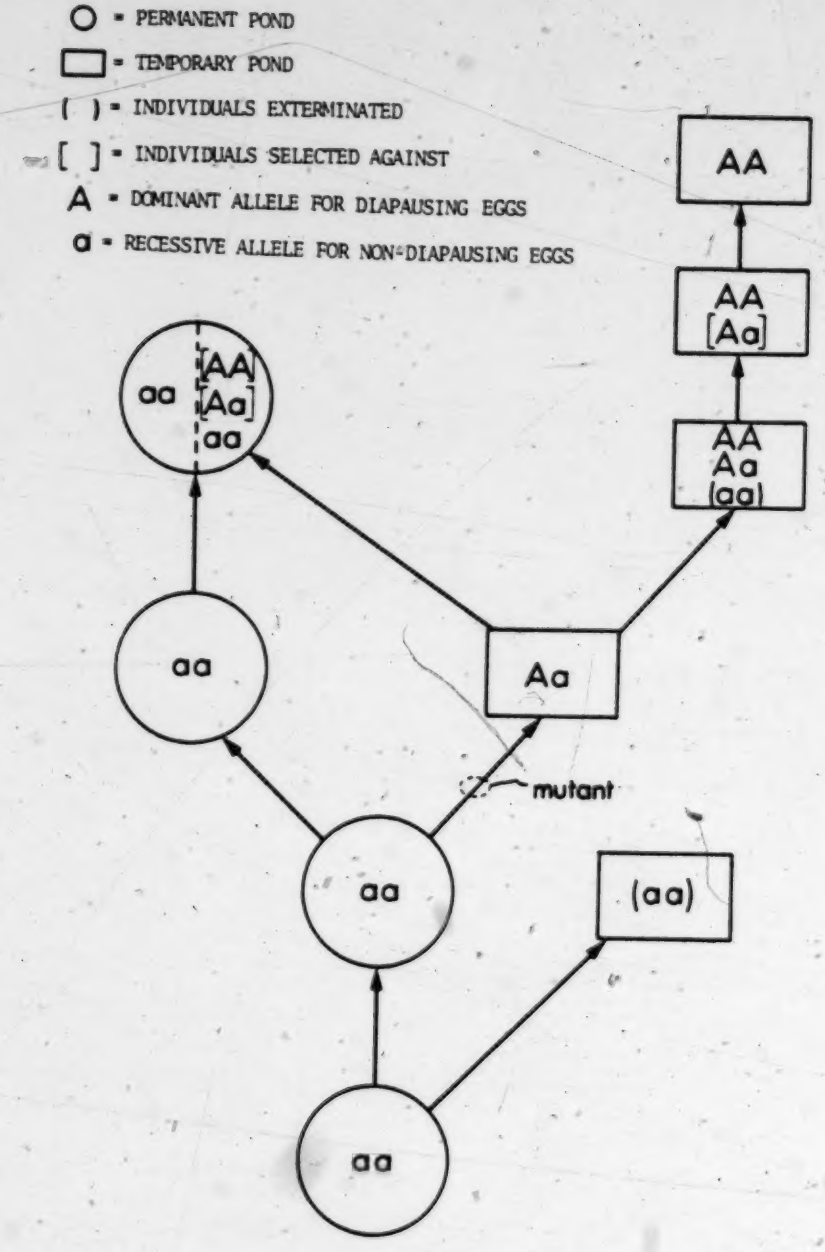


Figure 39. Schematic representation of events of sympatric speciation of lineages giving rise to Chaoborus trivittatus and Chaoborus cooki-nyblaei.

AUTOBIOGRAPHY

I was born July 1, 1953 in Enschede, Netherlands. My father's work led our family to emigrate to Canada in December, 1954. After two and a half years in Toronto and a stay in Rochester, New York of one year, we moved to Edmonton, Alberta where I completed my primary and secondary schooling.

I spent my younger years exploring swamps, meadows and woodlands and by the age of ten was seriously collecting butterflies. Further collecting led to additional groups, in particular those in aquatic habitats, and at the age of fourteen I became enraptured by the transparent larvae of Chaoborus species. I spent numerous hours collecting, observing and rearing these beautiful creatures. A term report written in Grade 10 and identification of larvae for Dr. D.M. Rosenberg, then a Ph.D. candidate in this department, directed my interests in a systematic direction.

Summer jobs during high school included two summers working for Dr. B.S. Heming of this department mounting thrips on microscope slides. I also worked weekends during my last two years of high school for Dr. G.E. Ball curating beetle material, preparing distribution maps and assisting in studies of geographical variation of carabid beetles.

In 1971 I began a four year B. Sc. with specialization in entomology at the University of Alberta. Summers during my undergraduate program were spent as a summer assistant under Dr. O.A. Saether, at the Freshwater Institute at Winnipeg, Manitoba, under

Dr. F. McAlpine at the Biosystematic Research Institute in Ottawa, Ontario and for the City of Edmonton mosquito control program. I completed my B. Sc. in April, 1975 and in May of that year began a masters program, the results of which are reported in this work.